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Breeding Ecology, Success, and Population Management of the Piping Plover (Charadrius melodus) at Chincoteague National Wildlife Refuge, Virginia

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BREEDING ECOLOGY, SUCCESS, AND POPULATION MANAGEMENT OF THE PIPING PLOVER (*Charadrius melodus*) AT CHINCOTEAGUE NATIONAL WILDLIFE REFUGE, VIRGINIA.

A THESIS

Presented to

The Faculty of the Department of Biology

The College of William and Mary in Virginia

In Partial Fulfillment

of the Requirements for the Degree of

Master of Arts

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by

Robert R. Cross

1996

APPROVAL SHEET

This thesis is submitted in partial fulfillment of the requirement for the degree of

Master of Arts

Robert R. Cross

Author

Approved, August 1996

Mitchell A. Byrd, Ph.D.

Stewart A. Ware, Ph.D.

Ruth A. Beck, M.Ed.

In memory of
Calvin L. Cross Sr.

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ABSTRACT

This study examined the population size, distribution, reproductive success, and behavioral processes of the Federally Threatened Piping Plover (Charadrius melodus) at Chincoteague National Wildlife Refuge, Virginia from 1989-1991. Piping Plovers were censused throughout the breeding season (March-October). Adults and pre-fledged juveniles were color banded in 1989.

The breeding population ranged from 32 pairs in 1989 to 42 pairs in 1990. Reproductive success (measured as chicks fledged/nesting pair/year) ranged from 0.57 in 1990 to 1.13 in 1989. Nesting density was greatest (mean = 4.3 nests/km) in the southernmost nesting area (the Hook) and a regular pattern of nest dispersion on the Hook indicates strong competition for resources there.

Predator exclosures, constructed around 102 Piping Plover nests, were successful in protecting eggs from predators. Nest abandonments were the greatest source of egg loss at exclosure treated nests. Abandonments increased each year. Evidence suggests that red foxes (Vulpes vulpes) associated the exclosures with food and caused most nest abandonments. Flooding was the next leading cause of egg loss.

Reproductive success was more severely limited during brood rearing than during incubation. Chicks that did not survive disappeared early, 68.2% in the first six days after hatching. Red foxes were responsible for most chick loss (35%). Ghost Crabs (Oncypoda quadrata) were responsible for 22.8% of all chick loss. Lethal predator controls were ineffective in curbing chick loss.

In oceanfront nesting areas, Piping Plovers consistently selected nest sites on the beach berm but showed an increasing tendency to select more vegetated sites behind primary dunes. A preference was detected for inner beach nest sites, closer to marshes and mud flats than to oceanfront wracklines. Man-made dune systems may limit the availability of nesting habitat in some areas of the refuge.

BREEDING ECOLOGY, SUCCESS, AND POPULATION MANAGEMENT OF THE PIPING PLOVER (*Charadrius melodus*) AT CHINCOTEAGUE NATIONAL WILDLIFE REFUGE

GENERAL INTRODUCTION

The piping plover (Charadrius melodus m. Ord.) is an endemic, migratory shorebird in North America and breeds in three disjunct geographic locations; in the Great Lakes region, the northern Great Plains, and along the Atlantic coast from Newfoundland to North Carolina (Johnsgard 1984, Haig and Oring 1985, USFWS 1988). Continent-wide populations of the piping plover have been decreasing since 1945 (Sidle 1984). Canada was the first country to recognize the seriousness of the decline, and declared the species as threatened in 1978 (Bell 1978), changing the status to endangered in 1985 (Goosen, J.P. 1990, Haig 1985). In January of 1986, the U.S. Fish and Wildlife Service formally listed the piping plover as endangered in the Great Lakes region and threatened throughout the remainder of its U.S. breeding range (Federal Register 1985) including the Atlantic coast where populations had declined an estimated 27 to 30 percent from 1980 to 1984 (Haig and Oring 1987). In 1991 an estimated 751 pairs of piping plovers were found on the U.S. Atlantic Coast (USFWS 1993). Haig (1992) estimated 2334 pairs remaining in the entire North American population in the same year.

The piping plover is now considered to be a valuable and effective indicator species, demonstrating the changeable nature of its coastal nesting habitat and the sensitivity of such habitats to human-related activities. Throughout their range, piping plovers are among the first species to exhibit the detrimental effects of habitat alterations (Haig and Oring 1987). Loss of habitat, disturbance during the breeding cycle, and escalating predation have been identified collectively as factors limiting piping plover breeding success (Cairns and McLaren 1980; Burger 1987; Flemming et al. 1988; Haig and Oring 1985, 1987; Robertson and Flood 1980; Sidle 1985; USFWS 1988; Williams et al. 1988; and others).

Before the listing of the piping plover as an endangered/threatened species in 1986, almost all of the information on breeding for this species came from a single study (Wilcox 1959). Since then, numerous studies have been conducted throughout its range. However, the habitat requirements and factors limiting nesting success are still poorly understood (Haig 1992).

From 1988 through 1991 on the Atlantic coast, piping plover fledgling productivity averaged 1.14 chicks fledged per pair based on 461 ± 112.0 pairs per year (USFWS 1988a). Gaines and Ryan (1988) estimated an annual fecundity of 1.15 to 1.44 chicks fledged per pair as necessary to maintain a stable population in the northern Great Plains. On the Atlantic coast a similar annual fecundity of 1.245 chicks fledged per pair

was estimated as necessary for population stability (Melvin and Gibbs 1994).

In Virginia, the piping plover is mostly restricted as a breeding bird to the easternmost counties of Northampton and Accomack which encompass the barrier islands of Virginia's Eastern Shore. Small disjunct populations occur on the western shoreline of the Chesapeake Bay within the city of Hampton, Virginia (Akers 1975) and at a U.S. Army Corps of Engineers dredge spoil island along the shoreline of the Elizabeth River in Portsmouth, Virginia (R. Beck, pers comm.).

Historically, Virginia has supported a significant proportion of the Atlantic coast population; 12.5% in 1986 (Williams et al. 1988), and 11.6% in 1988 (USFWS 1988a). Population estimates for the piping plover in Virginia have remained stable in recent years relative to other Atlantic coast breeding areas. Plausibly, the protected status of the Virginia barrier islands is responsible for the stability (Williams et al 1988). Further, there may be a convergence of birds in mid-Atlantic states as a result of excessive habitat loss at the northern and southern extremes of their breeding range (Haig and Oring 1985).

Chincoteague National Wildlife Refuge (CNWR) is a vital breeding area for the piping plover, and regularly accommodates a substantial portion of the Virginia breeding population; 31.0% in 1988 (USFWS 1988b) and 27.0% in 1989 (this study). Only Metompkin Island, south of Chincoteague

NWR, may support larger numbers of breeding piping plovers in Virginia (39.7% of the Virginia population in 1989 according to Virginia Department of Game and Inland Fisheries surveys)(Virginia Department of Game and Inland Fisheries 1989).

In 1988, a piping plover monitoring and management program was initiated at Chincoteague NWR on Assateague Island. Management procedures included predator controls, and the employment of predator exclosures on 50% of all piping plover nests. Further, an Environmental Assessment for the management of piping plovers at Chincoteague NWR precipitated the closure of Toms Cove Hook and restricted access to pedestrian traffic in other nesting areas from 15 March through 31 August (USFWS 1988c). Nesting productivity improved by 342% over 1987 estimates (USFWS 1988b).

In 1989, a Memorandum of Agreement (MOA) between the U.S. Fish and Wildlife Service (USFWS) and the Virginia Department of Game and Inland Fisheries (VDGIF) facilitated the beginning of this three year management and research program of piping plover breeding biology at CNWR.

The objectives of this study are to quantify and analyze the seasonal and long term variation of predation, habitat quality (requirements), and behavioral processes as important components of successful breeding in the piping plover and to identify those factors which are limiting or which threaten nesting success for this species at CNWR. I also collected

data to determine the specifics of piping plover breeding ecology in Virginia. I attempted to incorporate the annual findings of this study into a successful management program for piping plovers nesting at Chincoteague NWR through cooperation with land managers and wildlife officials.

SPECIES DESCRIPTION

The piping plover is the palest of the ringed plovers found breeding in Virginia. It is a small shorebird, 17-18 cm long (Haig 1992), with an average weight of 53.6 g (n = 70, range = 46.5 - 62.0, Loegering 1992), pale grayish brown above and white below with orange legs and a short, stubby, orange bill tipped with black. In alternate plumage, piping plovers have a single, black neck band which may be complete or incomplete, and a black brow bar. Adult females have a blackish-brown breast band and brow bar (Johnsgard 1981). Males and females exhibit a complete white band across the upper tail coverts in flight (Haig 1992).

In basic plumage the breast band is reduced to pale lateral patches, the brow bar is absent, and the bill and legs are duller (Palmer 1967). Juveniles resemble winter adults until first nuptial molt at one year of age.

Differences in the extent and pattern of the breast band have been used to distinguish two geographic subspecies of the piping plover, Charadrius melodus melodus on the Atlantic

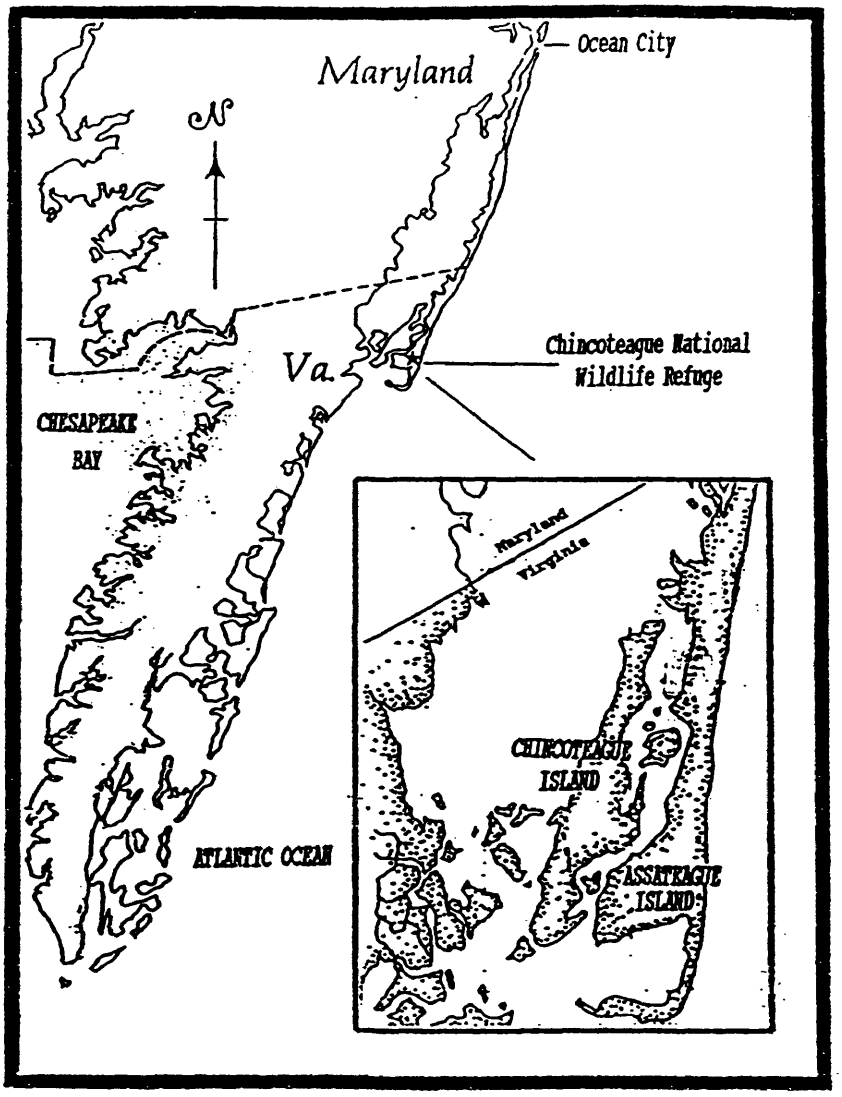
coast and Charadrius melodus circumcinctus in the northern Great Plains and Great Lakes populations. But no genetic differences have been found between Atlantic and inland populations and subspecific classification appears to be unwarranted (Haig and Oring 1988).

The Wilson's plover (Charadrius wilsonia), which may compete with piping plovers for nesting habitat and thus influence the spacing of piping plover nests on the Virginia barrier islands (Bergstrom and Terwilliger 1987), is larger and darker than the piping plover and has a much longer and heavier dark bill.

STUDY AREA

Chincoteague National Wildlife Refuge is located in Accomack County, Virginia on Assateague Island (see map, Figure 1.1). Assateague Island (37° 57′ N, 75° 21′ W) is an offshore barrier island on the southeastern coast of the Delmarva Peninsula. The island spans the Virginia/Maryland state line and is approximately 63.0 km in total length with 37.0 km located in Maryland and the remainder in Virginia. Assateague Island varies in width from about 2.0 km to 5.0 km and is separated from the mainland by Sinepuxent Bay to the north and Chincoteague Bay to the south. A causeway connects the mainland with Chincoteague and Assateague Islands. The refuge consists of 10,413 acres (4,214 hectares), nearly

Figure 1.1. Location of Chincoteague National Wildlife Refuge, Assateague Island, Virginia.


Maryland
Ocean City
N
Va.
Chincoteague National
Wildlife Refuge
CHESAPEAKE
BAY
ATLANTIC OCEAN
Maryland
Virginia
CHINCOTEAGUE
ISLAND
ASSATEAGUE
ISLAND

the entire Virginia portion of Assateague Island. In 1965, Assateague Island National Seashore was established.

Heaviest visitation to the refuge occurs in the summer months for the purpose of recreation, primarily at a 1 km section of beach known as the Public Beach, where parking and public facilities are provided. Administrative responsibilities at Chincoteague NWR are shared by the National Park Service, which manages public recreational use of designated areas, and the U.S. Fish and Wildlife Service which oversees all wildlife management.

Restrictions on the use of off-road vehicles (ORVs) at Chincoteague NWR first occurred in 1963 when the construction of a boundary fence at the northern border of the refuge eliminated ORV access to the refuge from the Maryland portion of Assateague (USFWS 1978). However the lower 8.05 km of the refuge remained open to ORVs year-round until 1988. At that time, a 2.4 km section of beach adjacent to the southern end of the Public Beach was established as an ORV zone where public ORV use is allowed, but not to exceed 18 vehicles at any one time. These regulations are currently in effect.

On Chincoteague NWR, four broadly delineated vegetational zones are present. These are (1) a beach/dune zone (2) shrub zone (3) pine or mixed pine/deciduous zone, and (4) salt marsh. These zones vary greatly in extent and are frequently interspersed with specialized communities such as fresh water vernal pools, salt pans, barrier flats, and fresh or brackish

water man-made impoundments. Piping plovers typically nest only in the first (beach/dune zone), although occasionally some birds select nest sites within thick vegetation representing a broad transitional ecotone between the beach/dune zone and the shrub zone. One large artificially-made water impoundment, which is dry during the summer months, is also used for nesting by piping plovers.

Within the beach/dune zone of Chincoteague NWR, an artificial dune system was constructed in 1963 to stabilize the low primary dunes and to allow plants of low salt tolerance to colonize new areas. The beach/dune zone varies in width from only a few meters in some northern sections of the beach to greater than 300 meters near the southern tip. American beachgrass (Ammophila breviligulata) is the dominant plant in this zone and is often associated with salt meadow hay (Spartina patens). A variety of forbs are present in lower abundance including seaside goldenrod (Solidago sempervirens), sea rocket (Cakile edentula), sandbur (Cenchrus tribuloides), marsh fleabane (Pluchea purpurascens), morning glory (Ipomoea), and wild bean (Strophostyles helvola). Common reed (Phragmites australis) may encroach in some areas (Nomenclature based on Silberhorn 1982).

Piping plovers nest on the southernmost 5.63 km of Chincoteague NWR known as Toms Cove Hook (Hook), on a 6.44 km section of the northern beach (Wild Beach), and on the floor of a 2.66 km x 0.81 km, seasonally-drained waterfowl

impoundment, North Wash Flats Impoundment (Wash Flats). Public use of the Wild Beach is limited to pedestrian use in the intertidal zone and is very light. The Hook and Wash Flats are closed to all public use during the piping plover nesting season. These three areas, representing the main study sites, differ markedly in habitat structure, food resources, and predator pressures. They also differ in nesting density and nesting success. All three sites are subject to harsh environmental conditions.

The Hook beach (Figure 1.2) is a wide, flat peninsula which separates the Atlantic Ocean from Tom's Cove and is bounded to the southwest by Chincoteague Inlet. As a down drift beach in close proximity to Chincoteague Inlet, the Hook is dynamic in its sediment budget, subject to long term accretion followed by episodic erosion. The result is a broad, unstable, sparsely vegetated beach, characterized by low dunes and frequent tidal flooding. Overwash fans and washout areas between dunes on the Hook provide desirable nesting habitat for piping plovers, while tidal pools, moist barrier flats, mud flats, and intertidal ocean edges provide a wide variety of productive foraging habitats. American beach grass dominates the plant community in the beach/dune zone on the east side of the Hook but gives way to wax myrtle (Myrica cerifera), which dominates the shrub zone in the central and western portions of the Hook. No upland zone is present on the Hook and only scattered salt marsh is found there.

The Wild Beach (Figure 1.3) is typically narrow and relatively stable due to the balance between erosion by longshore currents and beach replenishment from eolian transport (Leatherman 1976). Tall, man-made dunes now represent the primary dune system and breaches in the dune line are infrequent. Backdune areas on the Wild Beach, protected from wind and salt spray by tall dunes have become thickly vegetated with American beach grass. Notably, beach heather (Hudsonia tomentosa) appears in backdune regions of the Wild Beach indicating the general stability of the dunes. Foraging habitat for piping plovers nesting on the Wild Beach is limited to ocean edge intertidal areas as a result of dune stability which has prevented the formation of moist interdunal habitats.

The Wash Flats (Figure 1.3) is an expansive fresh water impoundment used by nesting piping plovers. Beginning in the early spring, fresh (or slightly brackish) water is drained from the Wash Flats through several water control structures so that by the beginning of the nesting season, water remains only in a narrow trough on the west side of the impoundment. The rate of drainage, however, is variable depending on local rainfall which can quickly re-flood the impoundment. Vegetation on the impoundment floor is absent in the spring but gradually increases throughout the nesting season. Vegetation becomes densest wherever the water table remains close to the surface. Dominant plant species on the wash flats

are three square sedge (Scirpus olneyi) and glasswort (Salicornia sp.). The Wash Flats is separated from the Wild Beach by a wide (200-300 m) shrub zone dominated by (Myrica cerifera) and groundsel (Baccharis halimifolia) with extensive fields of salt meadow hay. Foraging opportunities for piping plovers on the wash flats are dependent on water levels which likely determine prey activity.

Figure 1.2. Toms Cove Hook (Hook) study area.

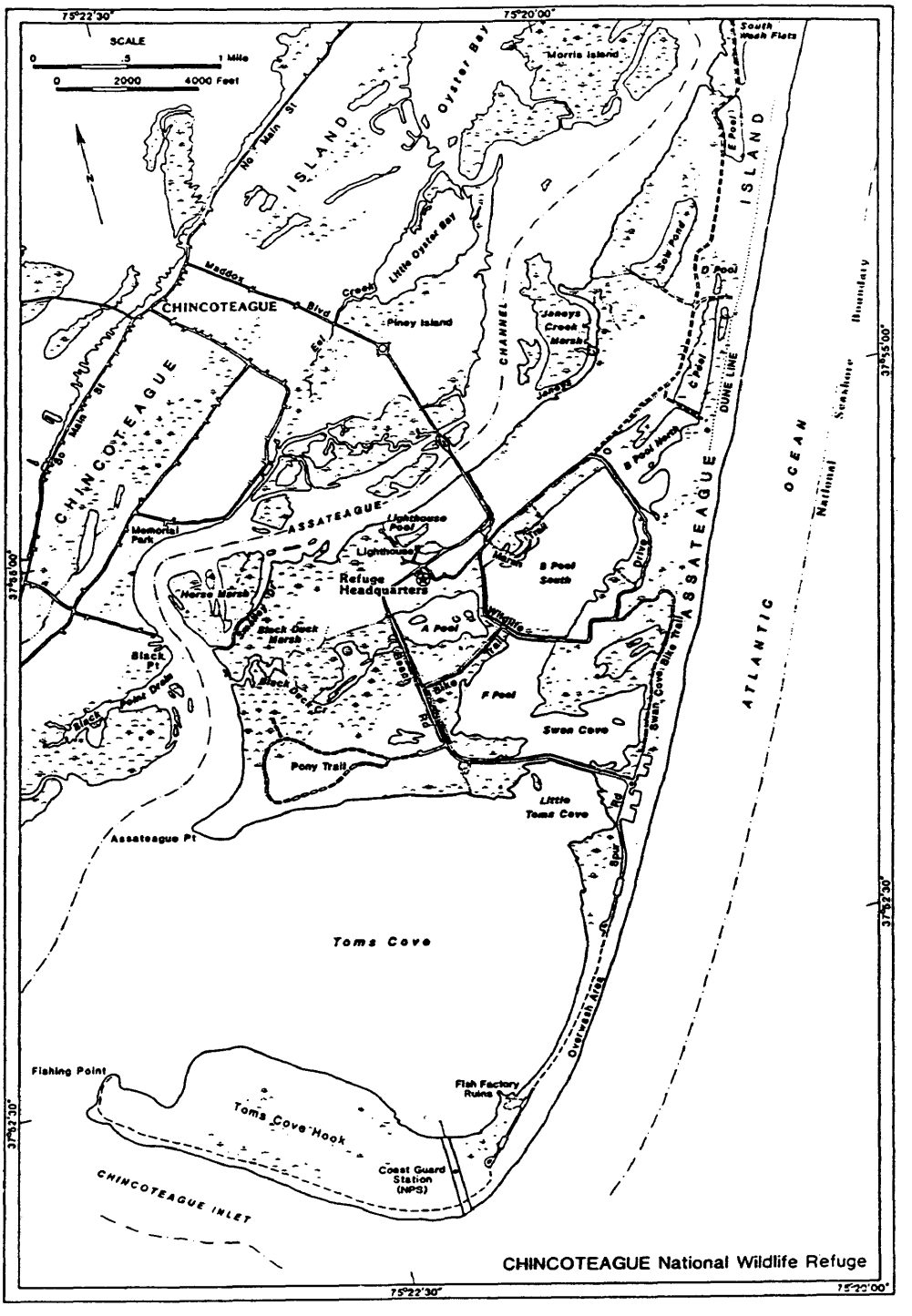
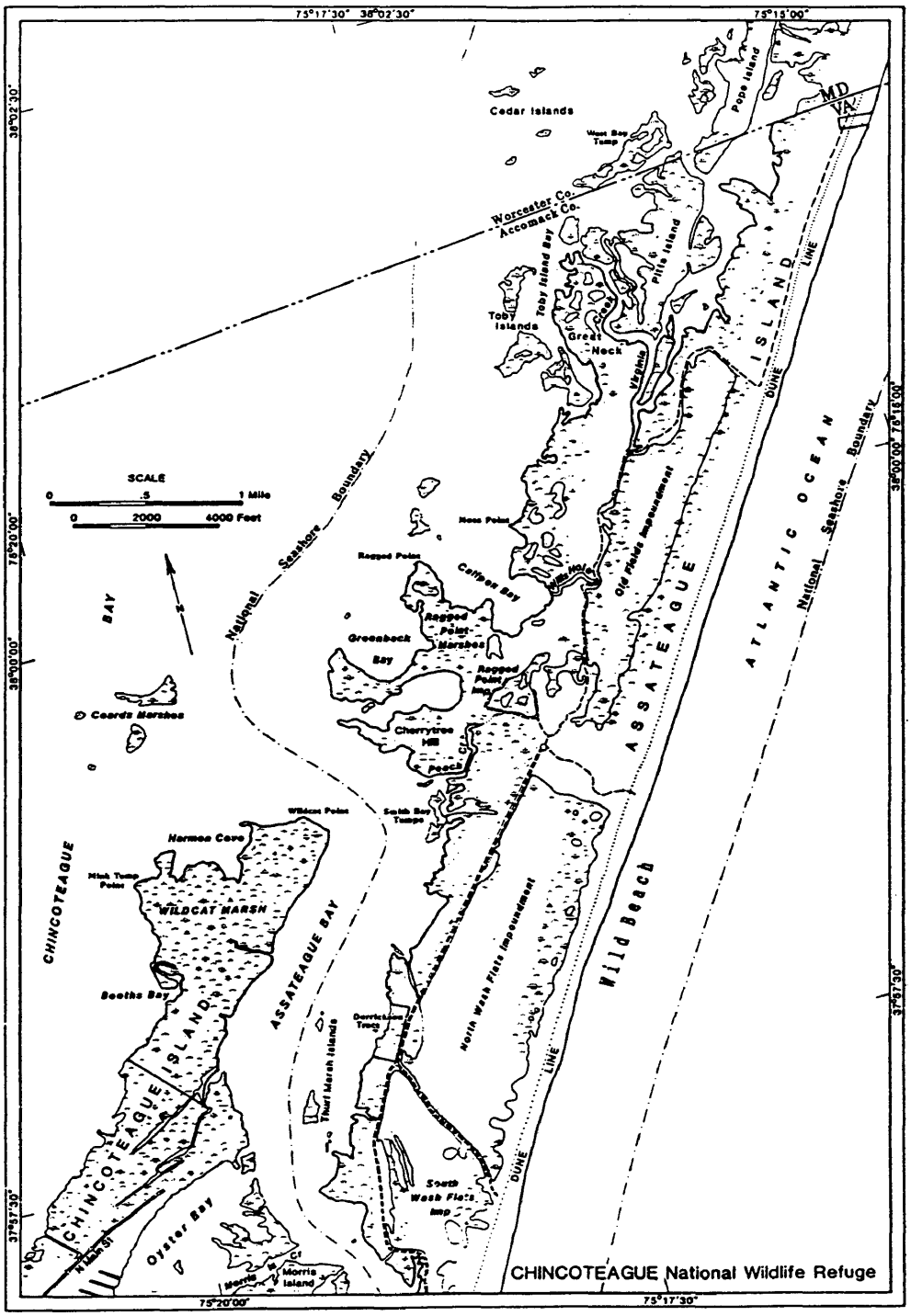

75°22'30"
75°20'00"
SCALE
0 .5 1 Mile
0 2000 4000 Feet
N
ISLAND
Oyster Bay
Morris Island
South Wash Flats
No. Main St
Little Oyster Bay
Creek
Waddox
Blvd
CHINCOTEAGUE
Piney Island
Ent
CHANNEL
Jeanys Creek Marsh
Jeanys
E Pool
Sob Pond
ISLAND
C Pool
DUNE LINE
B Pool Marsh
CHINCOTEAGUE
ASSATEAGUE
Memorial Park
Lighthouse Pool
Lighthouse
Refuge Headquarters
Horse Marsh
Loop Rd
Black Duck Marsh
B Pool South
Entrance Rd
A Pool
Wildlife Dr
Black Pt
Point Drake
Black Duck Cr
Bike Trail
F Pool
Swan Cove
Swan Cove Bike Trail
ASSATEAGUE
ATLANTIC
OCEAN
National Seashore Boundary
Pony Trail
Little Toms Cove
Assateague Pt
Toms Cove
Overwash Area
Fishing Point
Toms Cove Hook
Fish Factory Ruins
Coast Guard Station (NPS)
CHINCOTEAGUE INLET
CHINCOTEAGUE National Wildlife Refuge
37°52'30"
37°45'00"
75°22'30"
75°20'00"

Figure 1.3. Wild Beach and North Wash Flats Impoundment (Wash Flats) study areas.


CHINCOTEAGUE National Wildlife Refuge
CHINCOTEAGUE ISLAND
ASSATEAGUE ISLAND
ATLANTIC OCEAN
Wild Beach
ASSATEAGUE BAY
WILDCAT MARSH
Oyster Bay
Cedar Islands
Pope Island
Toby Island
Great Neck
Ragged Point
Greenbackers Bay
Cherrystone Hill
Morris Island
Thurl Marsh Islands
South Wash Flats Imp
North Wash Flats Impoundment
Old Plains Impoundment
Worcester Co.
Accomack Co.
National Seashore Boundary
DUNE LINE
MD
VA
SCALE
1 Mile
4000 Feet
75°17'30"
38°02'30"
75°15'00"
38°00'00"
37°57'30"
75°20'00"

PART 1. BREEDING ECOLOGY AND SUCCESS

Piping plovers breed on the Atlantic coast from Newfoundland to North Carolina (USFWS 1988, Cooper 1990). Their breeding range has changed little in this century although they may have retreated from former breeding sites in South Carolina (Haig and Oring 1987). They may have been common summer residents on the mid-Atlantic coast at one time (Bent 1929, Dyer 1987) but it is generally agreed that their numbers were alarmingly low around 1900 (Dinsmore 1981) mostly due to overgunning. Accurate population estimates, however, did not exist prior to 1980 (Haig and Oring 1987).

Piping plovers migrate to Virginia in March or April (Bent 1929) and have been observed in Virginia in all months except January (H. Armistead, pers. comm., C. Vaughn, pers. comm., Cross, pers. observ.). Fall migration occurs from July through September, peaking in August. Birds from the mid-Atlantic coast likely spend the winters farther south along the coast from South Carolina to Florida (Haig and Oring 1987). Nicholls and Baldassarre (1990) reported a preference of winter piping plovers for sand flats and mud flats near ocean inlets.

Piping plovers are solitary or sometimes semi-colonial nesters (Cairns 1977, Haig 1992). The nest is a shallow scrape, typically lined with bits of broken sea shells, constructed in the dry open areas of fine sand beaches or in sparsely vegetated and ephemeral dune slopes, overwashes, and island points (Cairns 1982).

Clutch size is almost always four eggs (Cross 1991, Loegering 1992). A nest from Cobb Island, Virginia contained five eggs (D. Bradshaw, pers comm.). Females lay an egg every other day until the clutch is complete (Haig 1988). Incubation is shared by both parents and lasts for 25 to 31 days (Cairns 1977, Weins 1986).

Hatching occurs from May through July, peaking in June in Massachusetts (MacIvor 1990). Piping plovers re-nest frequently after nest failure. Although only one brood is raised per year, they may raise another brood if the first is lost before fledging (Lapin and Sarr 1987, D. Rimmer, pers. comm.). One pair in Nebraska raised two broods (USFWS 1988d). Young fledge in 20 to 32 days (Haig 1987a).

This section presents information on abundance and breeding ecology of the piping plover from their arrival through departure at Chincoteague NWR. Long range trends in their distribution and nesting success on the refuge are also quantified.

METHODS

Piping plover activity was monitored in this study from the earliest date of their arrival at Chincoteague NWR in the spring until their departure in the fall of 1989, 1990, and 1991. A variety of professional and semi-professional biologists, field technicians and volunteers assisted me in this project throughout its three year duration. As the principle investigator, I contributed an estimated total of 6,960 individual hours of field work (mean = 2,320 ± 246.5 hrs., n = 3 yrs.) to duties related to piping plover research. This does not include time devoted to planning, analysis of the data, and reporting of the results.

POPULATION MONITORING AND BEHAVIORAL SURVEYS

Daily surveys were initiated on 1 March of each year to locate all piping plovers on the refuge and determine their breeding status. Surveys were conducted in all potentially suitable nesting habitat on foot and from four-wheel drive vehicles by traversing linear transects parallel to the oceanfront in beach nesting areas on the Hook and the Wild Beach and parallel to the eastern edge of the Wash Flats nesting area. Binoculars and 20x spotting scopes were used to locate and observe piping plovers.

Upon encountering piping plovers, data was collected regarding their location, sex, group size, activity (resting, foraging, courtship, nesting, other), and individual identification through the presence of color bands from this study or previous studies. Observations of courtship behavior, especially scrape-building and courtship flights, were later helpful in determining nesting territories and locating nests, since these behaviors are used to advertise nesting territories (Cairns 1982, Haig 1992, Haig and Oring 1987a).

Surveys were also used to familiarize researchers with predator activity in each nesting area and to record any occurrence of predator attacks on piping plovers. Surveys were conducted less frequently as the season progressed when more time was devoted to searching for nests in late April and May. Surveys were then discontinued in June and re-established in August after most breeding activity had ceased.

NEST SEARCHES

Nest searches were conducted beginning in mid-April whenever piping plovers exhibited territorial behaviors (Cairns 1982). Nests were typically located by observing birds from a distance until one adult returned to a nest and resumed incubation. Nests were also located, however, by following piping plover tracks in the sand until they converged in dense

paths near the nest. In some cases nests were located by chance while searching suitable habitats on foot.

Nest searches were limited to fifteen minutes in any given area and were not conducted during midday heat or in adverse weather in order to avoid thermal stress to uncovered eggs. Charadrii nesting in climates above 45°C often must incubate to cool the eggs rather than heat them (Bergstrom 1989).

Nests were marked by placing numbered wooden "painters sticks" no closer than 10 M from the nest. Nest locations were also plotted on 1:24,000 topographic maps. Data forms were used to record the nest numbers, location, substrate, adult identification, and number of eggs, and nesting attempt (initial or re-nest). Re-nesting attempts were determined by observing color banded individuals defending or incubating a nest after losing a prior nest or, in some cases, by finding a new nest close to a failed nest within two weeks of the initial nest failure.

Predator exclosures were used to protect some but not all nests in this study. Their use was determined primarily by differing predator pressure in each nesting area. In 1989, predator exclosures were slated for 100% of all nests on the Hook and 50% of all nests on the Wild Beach and Wash Flats. In 1990 and 1991, predator exclosures were prescribed for all piping plover nests found at Chincoteague NWR. Predator exclosures were constructed when the nest was located or when

the third egg was laid. Their construction and use is fully described in Part 2.

NEST MONITORING

I monitored piping plover nests every day until the clutch was complete by approaching only close enough to count the eggs through binoculars. Nests were then monitored every second or third day until hatching in order to assess the source of any egg loss. Hatching dates were predicted using 27 days from the laying of the last egg as an estimated incubation period. Whyte (1985) found a mean incubation period of 28 days for piping plovers in Nova Scotia, but Haig and Oring (1988b) found a mean incubation period of 25.7 days in Manitoba. Delayed incubation in shorebirds has been attributed to the time adults were kept off the nest by human intruders (Keighley and Buxton 1948) and to territorial interactions with neighboring pairs (Cairns 1982).

Nest monitoring provided information regarding clutch initiation dates. Since eggs are laid on alternate days (Cairns 1982, Wilcox 1959, Haig and Oring 1987a), clutch initiation dates were determined by back-counting 6 days from the date that the last egg was laid. If the clutch was complete when found, the clutch initiation date was calculated by back-counting 27 days from hatching to determine the date of clutch completion, then back-counting six more days.

Whenever eggs were discovered missing or if no adults were incubating for two consecutive nest checks, a search of the nest area was conducted to determine the cause of egg loss or abandonment. Egg predators were identified by tracks, burrows, examination of egg remains, feathers or other evidence left near the nest.

Nest monitoring provided the data necessary to calculate hatching success (number of eggs hatched per nesting pair of adults) and nesting success (number of nests hatching one or more eggs). Nest monitoring was also used to estimate the size of the breeding population in each nesting area.

BROOD MONITORING

I relocated broods daily after they left the nest until they reached 25 days of age. I considered chicks fledged if they were 25 days old or if I observed them in level flight prior to 25 days. Broods were not monitored after fledging but were included in population surveys during August and September.

Brood monitoring provided the data necessary to determine fledgling productivity as the number of chicks fledged per nesting pair.

BANDING ADULTS AND YOUNG

Adult and juvenile piping plovers were captured and banded for this study only in 1989 using standard aluminum, butt end, U.S. Fish and Wildlife Service bands (size 1A) and unique color band combinations (Buckley and Hancock 1967). All birds captured were banded on the metatarsus using no more than two bands per leg. Plastic color bands were made of ultra-violet stable (Darvik) material and were available in seven colors. A black and white pin-striped plastic band was used as the third color band and acted as an identifier for Chincoteague NWR. Plastic bands were attached by the application of a heated metal instrument to the band seam, melting the opposite edges of the seam together for permanent fixing. Banding schemes were coordinated with other Atlantic coast banding programs to ensure that no duplication of color combinations occurred. Piping plovers were previously banded at Chincoteague NWR in 1987 (Patterson 1988) and in 1988 USFWS 1988b).

Adult piping plovers were captured on the nest for banding using a wire framed, 12" x 12" x 6" box trap covered with 1" mesh fishing net (Dorio et al. 1978, Mills and Ryder 1979). A self-triggering device consisting of a line leading over the eggs caused the trap to fall when an adult resumed incubation. Adults were sexed by plumage, banded, weighed, and

morphometric data taken. They were then released at the point of capture and observed until incubation was resumed.

Pre-fledged chicks were captured by hand after they reached six days of age. They were weighed and banded in the same manner as the adults and then released all at once to their parents.

Color bands were useful in identifying individuals in the field without the need to recapture them. The process allowed computations of adult and juvenile return rates and greatly simplified brood observations leading to greater confidence in estimates of fledgling productivity.

RESULTS

POPULATION ESTIMATES

I found 32, 42, and 38 (mean = 37.3 ± 5.0) pairs of piping plovers nesting at Chincoteague NWR from 1989 to 1991, respectively. These figures represent 29.7% ± 3.7% (range = 26.4 - 33.6, n = 3 yrs.) of the Virginia piping plover population according to annual surveys by the Virginia Department of Game and Inland Fisheries (Table 1.1). The Number of birds nesting at Chincoteague NWR were not divided equally between the three nesting areas. More pairs of piping plovers were found nesting on the Hook (mean = 20.6 prs., SE

Table 1.1. Piping plover population trends, 1987 - 1991.

Population	Year	No. Of Pairs	Productivity Estimate
Chincoteague[1] NWR	1987	46	0.19
	1988	32	0.84
	1989	32	1.13
	1990	42	0.57
	1991	38	0.79
Virginia[2]	1987	100	---
	1988	103	0.67
	1989	121	1.13
	1990	125	0.65
	1991	131	0.88
U.S Atlantic[3] Coast	1987	570	1.04
	1988	644	1.11
	1989	724	1.29
	1990	717	1.06
	1991	704	---
N.A. Atlantic[4] Coast	1987	792	---
	1988	886	---
	1989	957	---
	1990	946	---
	1991	949	---

[1] Source of 1987 data; Patterson (1988), 1988 data; USFWS (1988b), 1989-1991 data; this study.

[2] All data from Virginia Department of Game and Inland Fisheries surveys (VDGIF 1987, 1988, 1989, 1990, 1991). 1988, 1990, and 1991 productivity estimates are weighted means from Chincoteague NWR, Craney Island and Grandview subpopulations. 1989 productivity estimate from Chincoteague NWR only.

[3] 1987 - 1990 data from U.S. Fish and Wildlife Service, Newton Corner, MA. 1991 data from Plissner and Haig (unpubl. data).

[4] 1987 - 1990 data from U.S. Fish and Wildlife Service and Canadian Wildlife Service. 1991 data from Plissner and Haig (unpubl. data).

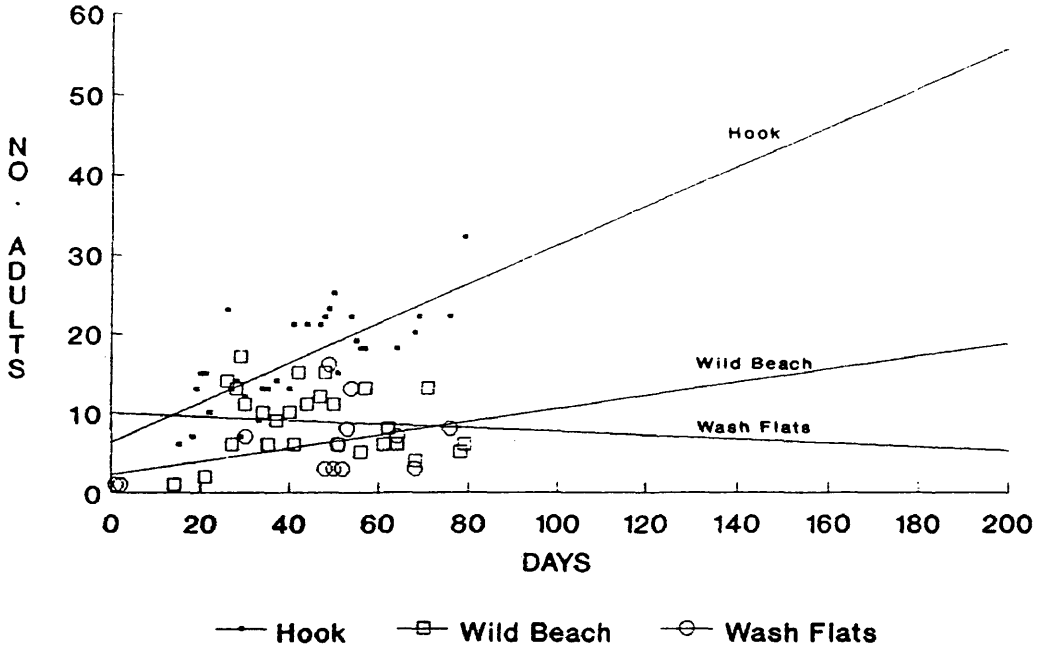
= 1.2, range = 19 - 23) than on the Wild Beach (mean = 9.6, SE = 1.8, range = 7 - 13) or the Wash Flats (mean = 7.0, SE = 1.0, range = 6 - 9) and the difference was significant (Kruskal Wallis chi-square approximation = 6.31, P = 0.0427, df = 2).

Numbers of piping plovers found on the Hook increased throughout the season in all three years (Figures 1.4, 1.5, 1.6) whereas numbers of birds found on the Wild Beach and the Wash Flats generally decreased in the late season. No late season surveys were conducted in 1989. Piping plovers on the Wild Beach and Wash Flats moved to neutral foraging areas on the Hook after fledging young or after failed nesting attempts.

More piping plovers were found on the Hook in surveys during all months and all years (mean = 19.0, SE = 1.1, n = 97) than were found on the Wild Beach (mean = 8.5, SE = 0.5, n = 78)(t = 20.09, P < 0.001) or on the Wash Flats (mean = 5.9, SE = 0.7, n = 38)(t = 19.63, P < 0.001). On 21 July 1990, 87 piping plovers (64 adults, 23 juveniles) were observed in a survey on the Hook. This emphasizes the importance of the Hook not only as a nesting area but as a pre-migratory staging area for piping plovers from other areas.

Figure 1.4. Adult piping plovers observed in surveys at Chincoteague NWR, March - April, 1989. Day 1 = 1 March. Mean number of birds observed per survey; Hook, 16.8, SE = 1.1, n = 32 surveys; Wild Beach, 8.9, SE = 0.8, n = 27 surveys; Wash Flats, 6.1, SE = 1.3, n = 13 surveys.

Figure 1.5. Adult piping plovers observed in surveys at Chincoteague NWR, March - April, 1990. Day 1 = 1 March. Mean number of birds observed per survey; Hook, 21.3, SE = 2.3, n = 29 surveys; Wild Beach, 7.6, SE = 0.8, n = 28 surveys; Wash Flats, 5.1, SE = 0.9, n = 19 surveys.


NO. ADULTS
60
50
40
30
20
10
0
Hook
Wild Beach
Wash Flats
0 20 40 60 80 100 120 140 160 180 200
DAYS
Hook
Wild Beach
Wash Flats

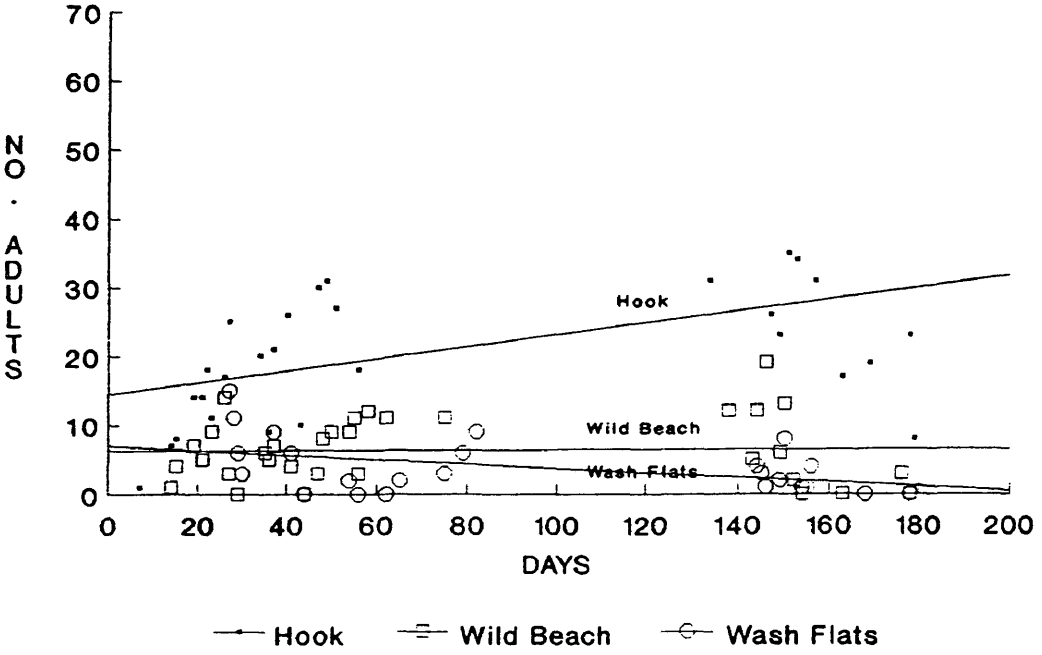
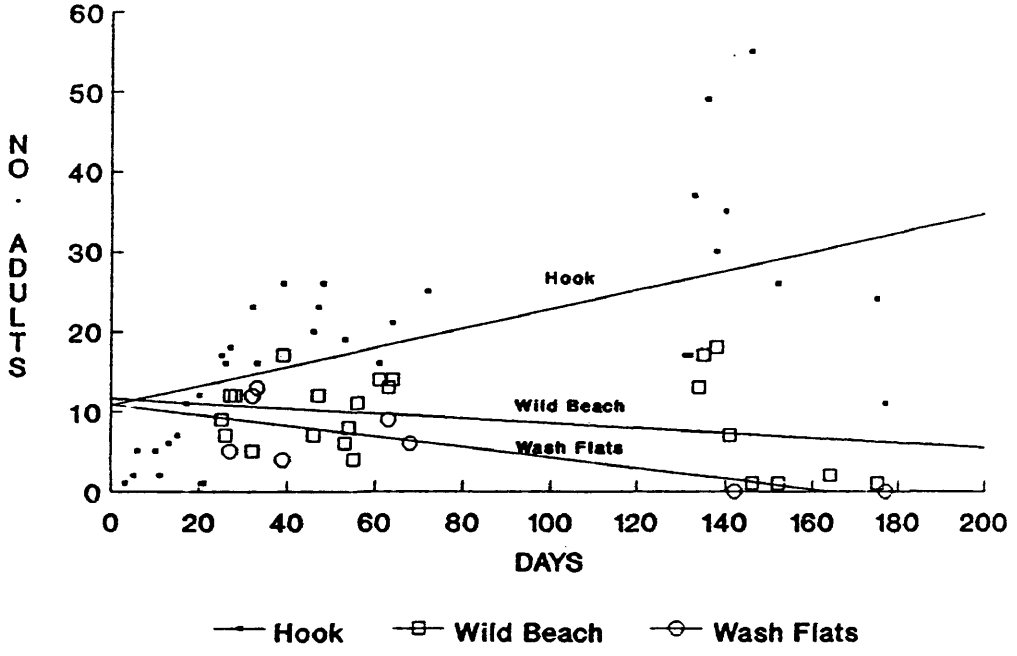

NO. ADULTS
70
60
50
40
30
20
10
0
Hook
Wild Beach
Wash Flats
0 20 40 60 80 100 120 140 160 180 200
DAYS
Hook
Wild Beach
Wash Flats

Figure 1.6. Adult piping plovers observed in surveys at Chincoteague NWR, March - April, 1991. Day 1 = 1 March. Mean number of birds observed per survey; Hook, 19.2, SE = 2.1, n = 36 surveys; Wild Beach, 9.2, SE = 1.1, n = 23 surveys; Wash Flats, 8.2, SE = 1.5, n = 6 surveys.


60
50
40
30
20
10
0
NO. ADULTS
Hook
Wild Beach
Wash Flats
0
20
40
60
80
100
120
140
160
180
200
DAYS
Hook
Wild Beach
Wash Flats

FORAGING SITE PREFERENCES

Piping plover foraging habitat preferences differed significantly on the Wild Beach and on the Hook in 1990 and 1991. In both years piping plovers on the Wild Beach were found more often foraging in intertidal areas adjacent to the surf than they were found foraging in any habitats away from the surf zone (1990, $P = 0.0013$; 1991, $P = 0.001$)(Table 1.2). This probably reflects the lack of profitable alternatives to foraging in the surf zone on the Wild Beach. On the Hook, foraging piping plovers were found significantly more often in the surf zone in 1991 ($P = 0.0282$) but not in 1990 ($P = 0.9719$). Piping plovers on the Hook often used a variety of alternative foraging habitats available to them.

Seasonal variation in the preference of foraging habitats was apparent only on the Hook (Table 1.3). In 1990, there were significantly more piping plovers foraging in the surf zone on the Hook in the early season than in the late season ($P = 0.0143$). In 1991, There were also more piping plovers foraging in the surf zone early in the season ($P = 0.0103$) and also more piping plovers foraging away from the surf zone in the later season ($P = 0.0552$). There were no significant changes in foraging habitat preference between early and late season on the Wild Beach in either year.

These differences in foraging habitat preference are taken as evidence of differences in the availability of

Table 1.2. Comparisons of the percentages of adult piping plovers observed foraging in the intertidal surf zone vs foraging sites away from the intertidal surf zone on the Hook and the Wild Beach, 1990, 1991. All season surveys included.

	% Foraging Surf			% Foraging Away			
	N	Mean	SE	N	Mean	SE	Probability. [1]
1990							
Hook	35	37.67	6.47	35	36.61	5.67	P=0.9719
Wild Beach	32	39.57	6.96	32	8.17	3.75	P=0.0013**
1991							
Hook	44	43.76	6.03	44	25.70	4.74	P=0.0282*
Wild Beach	33	41.51	6.87	33	6.0	2.10	P=0.0001***

[1] Wilcoxon two-sample Rank Sum test

* = $0.01 < P \leq 0.05$.
** = $0.001 < P \leq 0.01$.
*** = $P \leq 0.001$. These conventions will be followed throughout the tables and will no longer be explained in subsequent tables.

Table 1.3. Comparisons of the percentages of adult piping plovers observed foraging in the intertidal surf zone and foraging sites away from the surf zone in early season vs late season surveys, 1990, 1991. Early season ≤ 1 May. Late season > 1 May.

	Early Season Surveys			Late Season Surveys			
	N	Mean	SE	N	Mean	SE	Probability [1]
Hook 1990							
% Foraging Surf	20	51.27	8.61	15	19.55	7.85	P=0.0143 **
% Foraging Away	20	30.08	6.78	15	42.93	9.87	P=0.2571
Wild Beach 1990							
% Foraging Surf	19	47.83	9.54	13	27.50	9.39	P=0.1113
% Foraging Away	19	12.95	6.09	13	1.18	1.18	P=0.2479
Hook 1991							
% Foraging Surf	27	54.77	7.42	17	26.28	8.92	P=0.0103 **
% Foraging Away	27	17.99	5.12	17	37.95	8.55	P=0.0553
Wild Beach 1991							
% Foraging Surf	15	47.10	10.90	18	36.81	8.88	P=0.5036
% Foraging Away	15	5.14	2.59	18	6.72	3.24	P=0.9712

[1] Wilcoxon two-sample Rank Sum test

foraging habitats (therefore availability of prey) between study sites and as evidence of a shift in foraging site preference from the surf zone to sites away from the surf zone between early and late season on the Hook.

CHRONOLOGY OF THE BREEDING SEASON

Terms describing the activity phases of the breeding season are defined in Table 1.4. Most piping plovers arrived in early to mid-March. One male piping plover arrived at Chincoteague NWR on 24 February in 1990, but may have been a migrant. A mean early arrival date was calculated as 2 March ± 6 days (range = 24 February - 8 March, n = 3 yrs.).

Behaviors indicating territorial establishment and courtship including aerial displays, nest scrape building, and pre-copulatory displays were observed as early as 14 March, but foraging was the most common behavior observed in surveys during March of 1991 (86%). During April of 1991, however, foraging decreased to 150 of 285 observations (52.6%) and courtship activities were more frequently observed (86/285 observations, 30.2%). Copulations were observed frequently and were always performed within the nesting territory (n = 18 pairs, total = 3 yrs.) as indicated by the presence of nest scrapes or eggs.

Egg laying occurred from 21 April to 30 June (141 nests, 465 eggs, total = 3 yrs.) and was earliest in 1990. Piping

Table 1.4. Chronology of the piping plover breeding cycle at Chincoteague NWR, 1989-1991. See below for definitions of activity phases.

Activity Phase	Date
Early Arrival	24 February
Courtship	14 March - 21 April
Egg Laying	21 April - 30 June
Incubation	25 April - 22 July
Brood Rearing	22 May - 5 August
Late Departure	29 October

Activity Phase		Definition
Early Arrival	=	Earliest date observed at Chincoteague NWR.
Courtship	=	Period from earliest observation of courtship behavior to earliest clutch initiation.
Egg Laying	=	Earliest clutch initiation to latest clutch initiation.
Incubation	=	Earliest full time incubation to latest hatching date.
Brood Rearing	=	Earliest hatching date to latest fledging date.
Late Departure	=	Latest date observed at Chincoteague NWR.

plovers did not exhibit a consistent preference for early nesting areas. Egg laying was initiated earlier on the Hook in 1989 and 1990 but was earlier on the Wild Beach in 1991 (Figure 1.7).

Eggs hatched as early as 23 May in 1989 and as late has 22 July in 1990. The mean hatching date was 19 June (SE = 4.2 days, n = 91 nests, total = 3 yrs.) for all nests where hatching dates could be calculated. I could not determine when (time of day) eggs hatched since not all nests could be checked first thing in the morning. The laying period could only be determined if the nest was discovered with one egg and survived to four eggs (n = 16). The mean laying period was 7.1 days (n = 16, SE = 0.26, range = 6 - 10 days). I discovered most nests (32%) with complete 4 egg clutches (3 eggs, 21%; 2 eggs, 16%; 1 egg, 24%, n = 141). Eleven nests (8%) were confirmed only by finding broods of chicks. Fledging occurred as early as 14 June in 1989 and as late as 7 August in the same year.

Piping plovers were actively breeding with eggs or pre-fledged chicks for a mean of 16.7 weeks (range = 15 - 18, n = 3 yrs., Figures 1.8, 1.9, 1.10). Breeding activity usually peaked between weeks 9 and 10 (11 - 24 June) of the breeding season but in 1991 breeding activity peaked earlier at about 6 weeks (2 - 8 June). The number of active piping plover nests per week was similar between years considering all refuge nests (Table 1.5). There were, however, more active piping

Figure 1.7. Phenology of clutch initiation for piping plovers at Chincoteague NWR, 1989 - 1991. Horizontal lines represent duration of clutch initiation. Solid circles represent median clutch initiation date for each nesting area

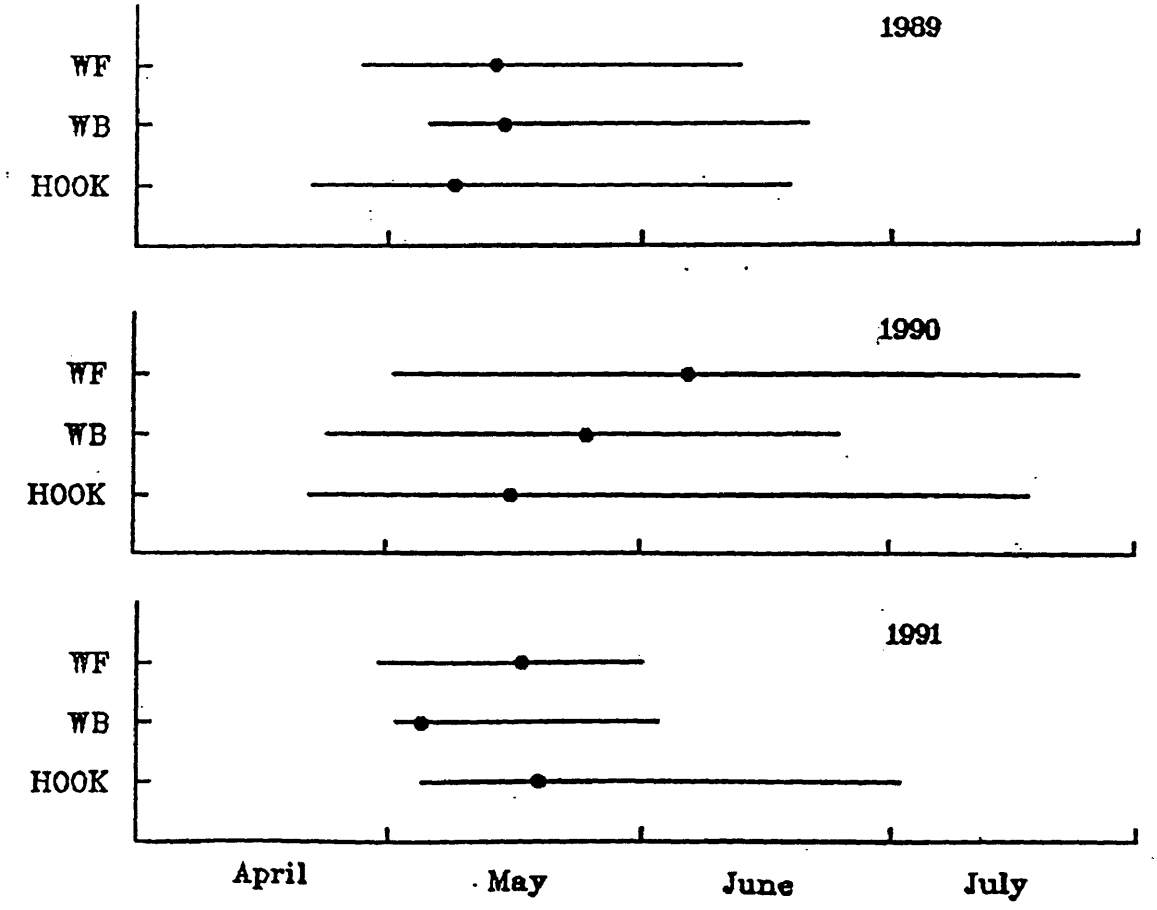
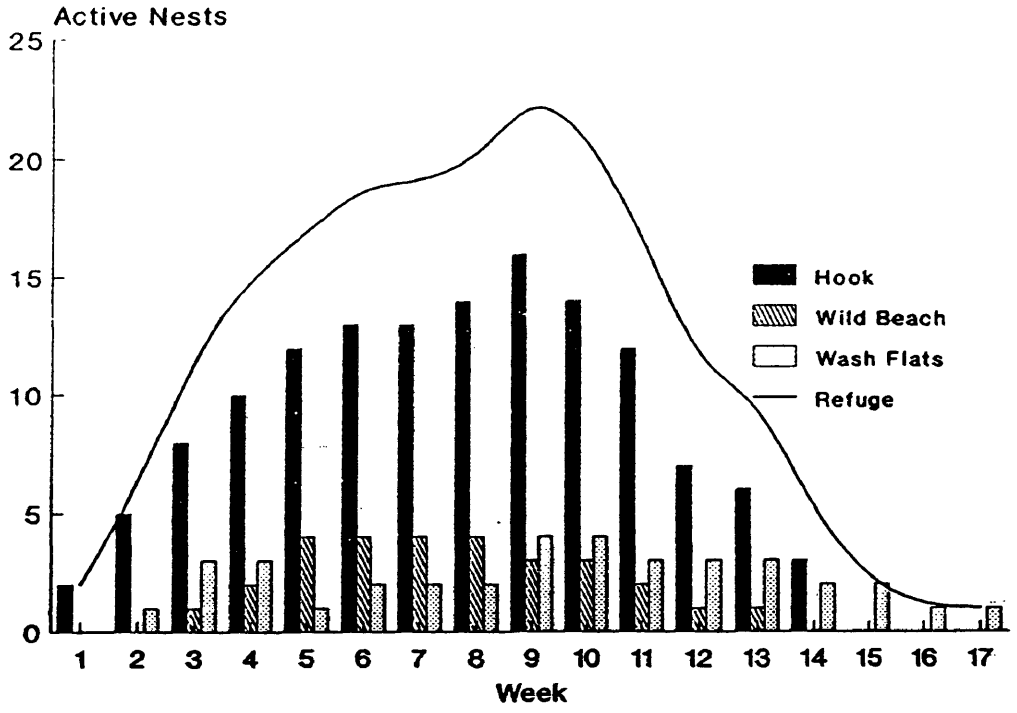

1989
WF
WB
HOOK
1990
WF
WB
HOOK
1991
WF
WB
HOOK
April
May
June
July

Figure 1.8. Number of active piping plover nests per week of breeding season, 1989.

Figure 1.9. Number of active piping plover nests per week of breeding season, 1990.


Active Nests
25
20
15
10
5
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
Week
Hook
Wild Beach
Wash Flats
Refuge

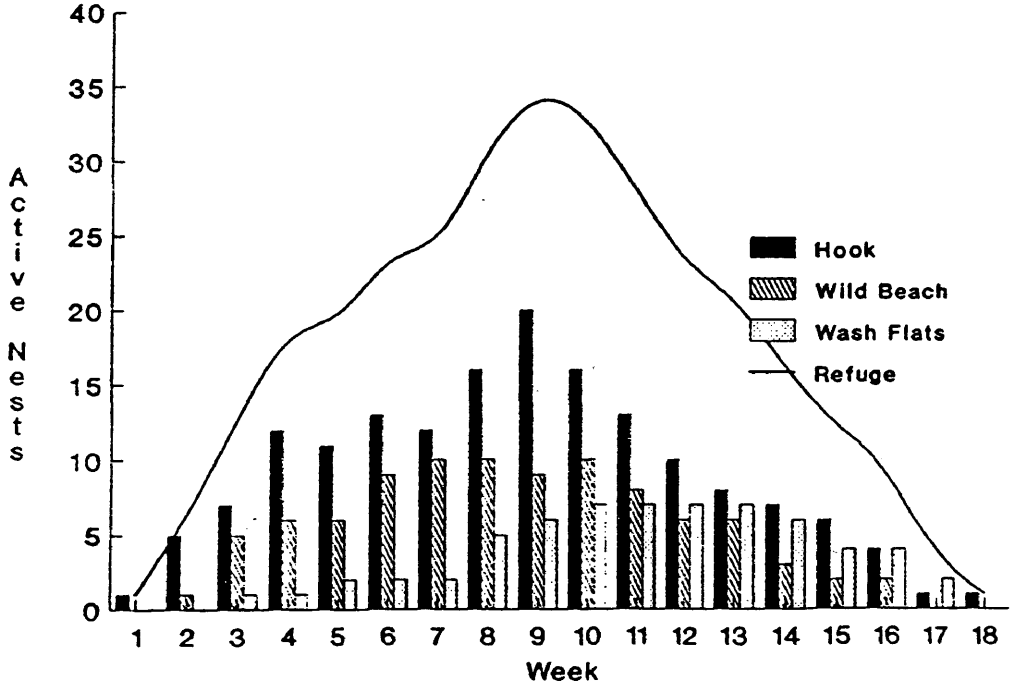

Active Nests
40
35
30
25
20
15
10
5
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Week
Hook
Wild Beach
Wash Flats
Refuge

Figure 1.10. Number of active piping plover nests per week of breeding season, 1991.

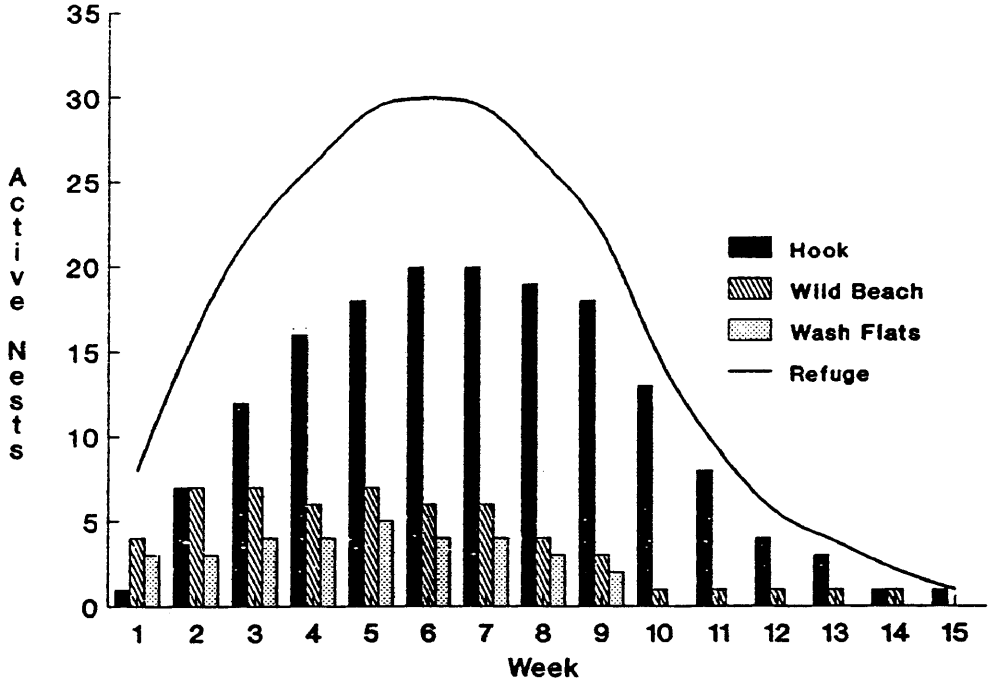

35
30
25
20
15
10
5
0
Active Nests
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Week
Hook
Wild Beach
Wash Flats
Refuge

Table 1.5. Descriptive statistics and comparisons [1] of the number of active piping plover nests per week in each nesting area and on the refuge, 1989-1991.

Area	Year	No. Weeks (N)	No. Nests / Week Mean	SD	Range
Hook	1989	17	7.94 A	5.53	0 - 16
	1990	18	9.06 A	5.56	1 - 20
	1991	15	10.73 A	7.52	1 - 20
		F = 0.815, P = 0.449, df = 49			
Wild Beach	1989	17	1.71 A	1.65	0 - 4
	1990	18	5.17 B	3.70	0 - 10
	1991	15	3.67 AB	2.66	0 - 7
		F = 6.577, P = 0.003 **, df = 49			
Wash Flats	1989	17	2.18 A	1.13	0 - 4
	1990	18	3.50 A	2.68	0 - 7
	1991	15	2.13 A	1.92	0 - 5
		F = 2.512, P = 0.092, df = 49			
Refuge	1989	17	11.82 A	7.72	1 - 23
	1990	18	17.72 A	10.75	1 - 35
	1991	15	16.53 A	10.97	1 - 30
		F = 1.528, P = 0.228, df = 49			

[1] One-Way Analysis of Variance
Means with the same letters are not significantly different (P > 0.05, Tukey HSD Multiple Comparisons).

plover nests per week in 1990 on the Wild Beach than in 1989 (One-Way ANOVA, P = 0.003).

NESTING PRODUCTIVITY

Hatching Success

Hatching success varied greatly between study areas and between years. I found a total of 465 eggs in 141 nests from 1989 to 1991 (Table 1.6). The hatching rate was 61.3% for all eggs. The percentage of eggs hatched was greatest on the Wild Beach (79.5%) and was lowest on the Wash Flats (48.0%) for all years. The greatest hatching success in any one year occurred on the Wild Beach in 1989 when 92.0% of all eggs hatched (n = 25). The lowest hatching success in any one year was found on the Wash Flats in 1991 when only 25.6% of all eggs hatched (n = 43).

Complete clutch size, defined as a nest with 4 eggs or a nest containing fewer than 4 eggs with no change in number for 3 consecutive days or until hatching, was determined to be 3.69 eggs/nest (SE = 0.60, n = 108, 3 yrs.). Complete clutch size was largest on the Wild Beach (3.84, SE = 0.10, n = 25) and was smallest on the Hook (3.61, SE = 0.09, n = 59). Observed nest success (≥ 1 egg hatched) of 4 egg clutches was not significantly greater than observed nest success at 3 egg clutches (G = 0.0902, P > 0.9, df = 1).

Table 1.6. Hatching and fledging success for piping plovers in three nesting areas at Chincoteague National Wildlife Refuge, 1989 - 1991.

Area	Year	Nests (N)	Nesting Pairs	Eggs Produced	No. Eggs Hatched (%)	Eggs Hatched/ Nest	No. Young Fledged (%)	No. Fledged/ Nesting Pr.
Hook	1989	20	19	75	52 (69.3)	2.60	22 (42.3)	1.15
	1990	33	23	91	36 (39.6)	1.09	16 (44.4)	0.70
	1991	25	20	83	58 (69.9)	2.32	19 (32.8)	0.95
	subtotal			249	146 (58.6)		57 (39.0)	
Wild	1989	8	7	25	23 (92.0)	2.88	4 (17.4)	0.57
Beach	1990	16	13	54	40 (74.1)	2.50	2 (5.0)	0.15
	1991	9	9	33	26 (78.8)	2.89	3 (11.5)	0.33
	subtotal			112	89 (79.5)		9 (10.1)	
Wash	1989	8	6	27	18 (66.7)	2.25	8 (44.4)	1.66
Flats	1990	10	6	34	21 (61.8)	2.10	6 (28.6)	1.00
	1991	12	9	43	11 (25.6)	0.91	8 (72.7)	0.89
	subtotal			104	50 (48.0)		22 (44.0)	
Refuge	1989	36	32	127	93 (73.2)	2.03	34 (36.6)	1.13
	1990	59	42	179	97 (54.2)	1.64	24 (24.7)	0.57
	1991	46	38	159	95 (59.8)	2.07	30 (31.6)	0.79
	subtotal			465	285 (61.3)		88 (30.9)	

The percentage of successful nests (hatching at least one egg) was also greatest on the Wild Beach (81.8%, n = 33) and was lowest on the Wash Flats (53.3%, n = 30) for all years. The difference in percentage of successful nests between nesting areas was significant ($X^2 = 19.95$, df = 2, $P < 0.001$). A total of 63.8% of all nests (n = 141) hatched successfully.

Fledging Success

A total of 88 (34, 24, 30) piping plover chicks fledged at Chincoteague NWR from 1989 to 1991 (Table 1.6). Fledging success was greatest in 1989 when 36.6% of all chicks (n = 93) fledged. But the difference in the percentage of chicks fledged between years was not significant based on the percentage of hatched chicks that fledged ($X^2 = 2.16$, df = 2, $P > 0.05$).

Fledging success varied between years and between study sites but was consistently lower than hatching success in all years and at all sites. Fledgling productivity was greatest in 1989 (1.13 chicks fledged per nesting pair) and was lowest in 1990 (0.57 chicks fledged per nesting pair). The lowest fledging success was found on the Wild Beach in 1990 when only 2 chicks fledged (0.15 chicks per nesting pair). Highest fledging success was recorded on the Wash Flats in 1989 when 8 chicks fledged (1.66 chicks per nesting pair).

Pre-fledged piping plover chicks generally remained close to the nest on the Hook and on the Wild Beach but travelled great distances from the nest on the Wash Flats. In 1991, broods on the Hook moved from 35 to 796 M (mean = 147.5, SE = 58 , n = 13) from the nest during the first week after hatching. Broods on the Wild Beach moved a mean of 59.0 M (SE = 11.6, n = 6, range = 35.0 - 100.0) and broods on the Wash Flats moved a mean of 463.7 M (SE = 181.3, n = 3, range = 150.0 - 778.0). There was a significant difference in the distance broods moved from the nest between the Wild Beach and the Wash Flats (Mann-Whitney U test, U = 21.0 , P = 0.0282).

Piping plover chicks that did not survive for 25 days typically disappeared early. For all piping plover chicks in three years where age at disappearance was known (n = 176) most (68.2%) disappeared within the first 6 days after hatching. Forty chicks (22.7%) disappeared on the day of hatching (day 1).

The mean disappearance age of pre-fledged chicks that did not survive to 25 days of age was greatest on the Wash Flats (6.44 days, SE = 1.16, range = 2 - 13) in 1989 (Table 1.7), the Wash Flats (6.87 days, SE = 1.56, range = 1 - 20) in 1990, and on the Hook (5.58 days, SE = 0.70, range = 1 - 13) in 1991. Further, the mean disappearance age of pre-fledged chicks was greater in 1990 (6.22 days, SE = 0.87, range = 1 - 20) than in other years. However, there were no significant differences in the mean disappearance ages of pre-fledged

Table 1.7. Comparison of mean disappearance ages (days) of pre-fledged piping plover chicks in all nesting areas at Chincoteague NWR, 1989 - 1991. Only chicks surviving 24 days or less are included in samples.

Sample	N	Mean	SE	Range	F	Probability [1]	df
1989							
Hook	30	5.30 A	0.94	1 - 21			
Wild Beach	14	5.86 A	1.51	1 - 22	0.196	P=0.577	52
Wash Flats	9	6.44 A	1.16	2 - 13			
1990							
Hook	25	6.84 A	1.08	1 - 19			
Wild Beach	29	3.86 A	0.75	1 - 19	3.033	P=0.055	68
Wash Flats	15	6.87 A	1.56	1 - 20			
1991							
Hook	34	5.58 A	0.70	1 - 13			
Wild Beach	19	3.37 A	0.57	1 - 8	3.123	P=0.052*	55
Wash Flats	3	3.33 A	0.33	3 - 4			
Refuge 1989	53	5.26 A	0.61	1 - 22			
Refuge 1990	67	6.22 A	0.87	1 - 20	0.855	P=0.427	177
Refuge 1991	56	4.64 A	0.48	1 - 13			

[1] ANOVA
Means with same letters are not significantly different (P > 0.05, Tukey HSD multiple comparison).

chicks between study areas or between years.

Only three times did all four chicks fledge from single broods. Most often, only one chick of the brood fledged (22 of 48 broods). The mean size of fledged broods was 1.79 chicks (SE = 0.13, n = 48, range = 1 - 4). Fledged broods were larger on the Wash Flats (mean = 2.0, SE = 0.23, n = 11) than on the Hook (mean = 1.89, SE = 0.18, n = 29) or the Wild Beach (mean = 1.13, SE = 0.13, n = 8). The difference was not significant (One-Way ANOVA, $F = 2.917$, $P = 0.064$, $df = 47$). A post-hoc comparison, however, showed that brood size was significantly larger on the Wash Flats than on the Wild Beach ($P = 0.017$, Tukey HSD, Tukey-Kramer Correction for unequal sample sizes).

Most chicks fledged from early season nests. Chicks were significantly more likely to fledge if the nest was initiated in the first 10 day interval of the breeding season in 1989 ($G = 10.5810$, $P < 0.005$) or if the nest was initiated in the second 10 day interval in 1991 ($G = 17.6340$, $P < 0.001$)(Table 1.8). In 1990, more chicks (66.7%) fledged from nests initiated after 21 May. But the difference in the number of chicks fledged throughout the nesting season was not significant in any 10 day period in that year.

Re-nesting

There were 32 nests that were determined to be re-nests in this study (Table 1.9). Most, 17 (53%) occurred in 1990 and

were the result of an extremely wet nesting season when many nests were lost to flooding. Only two pairs of piping plovers re-nested twice in a season and none re-nested a third time. Re-nesting was most commonly observed on the Hook. The time required to re-nest ranged from 4 days to 36 days. There were no observations of piping plovers raising two broods to fledging age, but there were two observations of re-nesting after losing an initial brood of chicks before fledging.

Only 4 pairs of re-nesting piping plovers (13%) shifted nesting areas between nesting attempts. One pair re-nested unsuccessfully on the Wash Flats after losing an initial brood of chicks to a raccoon on Assateague Island National Seashore in Maryland (J. Loegering, pers. comm.). Two pairs re-nested on the Wash Flats after a failed nesting attempt on the Hook. One pair re-nested on the Wash Flats after a failed nesting attempt on the Wild Beach. In 1990, the mean distance between initial nests and re-nests was 1,369 M (SE = 834 M, n = 16, range = 34 - 13,390), but this includes two pairs of piping plovers that changed nesting areas when re-nesting. For re-nests in the same nesting area as the initial nest, the mean distance between nests was 385 M (SE = 181 M, n = 14, range = 34 - 2685).

Clutch initiation dates were divided into six successive 10 day intervals for each year to determine the frequency of laying throughout the season (Table 1.10). Most nests were initiated prior to 21 May in 1989 and 1991 with significantly

Table 1.8. Analysis of frequencies by G test of the observed vs expected [1] number of piping plover chicks fledged from nests initiated in six successive ten day intervals at Chincoteague NWR, 1989-1991.

10 Day Interval		No. Of Piping Plover Chicks Fledged From Nests Initiated: Within Interval	Outside Interval	G	P
1989 (N=28)					
4/21-4/30	OBS.	12	16	10.5810	< 0.005
5/1-5/10	OBS.	9	19	4.0077	< 0.05
5/11-5/20	OBS.	1	27	4.8069	< 0.05
5/21-5/30	OBS.	5	23	0.0275	NS
5/31-6/9	OBS.	0	28	---	
6/10-6/19	OBS.	1	27	4.8069	< 0.05
	EXP.	4.67	23.33		
1990 (N=24)					
4/21-4/30	OBS.	4	20	0.00	NS
5/1-5/10	OBS.	2	22	1.4211	NS
5/11-5/20	OBS.	2	22	1.4211	NS
5/21-5/30	OBS.	4	20	0.00	NS
5/31-6/9	OBS.	7	17	2.3090	NS
6/10-6/19	OBS.	5	19	0.2823	NS
	EXP.	4.0	20.0		
1991 (N=30)					
4/21-4/30	OBS.	3	27	1.0909	NS
5/1-5/10	OBS.	15	15	17.6340	< 0.001
5/11-5/20	OBS.	7	23	0.8751	NS
5/21-5/30	OBS.	3	27	1.0909	NS
5/31-6/9	OBS.	1	29	5.3895	< 0.05
6/10-6/19	OBS.	1	29	5.3895	< 0.05
	EXP.	5.0	25.0		

[1] Expected frequencies are based on 5:1 ratios and are the same for all comparisons within year classes.

Table 1.9. Number of days from loss of nest or young to initiation of re-nesting attempt by the same breeding pair, 1989 - 1991.

Area	Year	Re-nests (N)	Number of Days to Re-nest n	Mean	SE	Range
Hook	1989	1	1	6.0	---	-----
	1990	10	10	14.7	2.9	5 - 36
	1991	7	4	14.0	6.7	6 - 34
Wild Beach	1989	1	1	---	---	-----
	1990	3	3	12.0	1.5	9 - 14
	1991	1	1	17.0	---	-----
Wash Flats	1989	2	2	6.5	2.5	4 - 9
	1990	4	2	8.5	0.5	8 - 9
	1991	3	1	11.0	---	-----
Refuge	1989	4	4	6.3	0.2	4 - 9
	1990	17	15	11.7	0.8	5 - 36
	1991	11	6	14.0	1.2	6 - 34

Table 1.10. Analysis of frequencies by G test of the observed vs expected [1] number of piping plover nests initiated in six successive 10 day intervals [2] at Chincoteague NWR, 1989 - 1991.

Time Interval		No. of Piping Plover Nests Initiated		G	P
		Within Interval	Outside Interval		
1989 (N=29)					
4/21-4/30	Obs.	8	21	2.1688	NS
5/01-5/10	Obs.	5	24	0.0071	NS
5/11-5/20	Obs.	6	23	0.3205	NS
5/21-5/30	Obs.	3	26	0.9378	NS
5/31-6/09	Obs.	1	28	5.0875	< 0.05
6/10-6/19	Obs.	6	23	0.3205	NS
	Exp.	4.83	24.17		
1990 (N=58)					
4/21-4/30	Obs.	10	48	0.0134	NS
5/01-5/10	Obs.	9	49	0.0568	NS
5/11-5/20	Obs.	7	51	0.9612	NS
5/21-5/30	Obs.	9	49	0.0568	NS
5/31-6/09	Obs.	13	45	1.2688	NS
6/10-6/19	Obs.	10	48	0.0134	NS
	Exp.	9.67	48.33		
1991 (N=38)					
4/21-4/30	Obs.	1	37	7.8200	< 0.01
5/01-5/10	Obs.	16	22	13.6430	< 0.001
5/11-5/20	Obs.	7	31	0.0828	NS
5/21-5/30	Obs.	7	31	0.0828	NS
5/31-6/09	Obs.	5	33	0.0828	NS
6/10-6/19	Obs.	2	36	4.6181	< 0.05
	Exp.	6.33	31.67		

[1] Expected frequencies based on 5:1 ratios. df=1 in all comparisons.
[2] Range of clutch initiation = 1989, 4/21-6/19; 1990, 4/21-6/23; 1991, 4/29-6/30.

fewer than expected clutch initiations in interval 5 in 1989 ($G = 5.0875$, $P < 0.05$) and significantly more clutch initiations than expected in interval 2 in 1991 ($G = 13.6430$, $P < 0.001$). This suggests that there was a strong initial nesting season in those years with some re-nesting in the mid-season. But in 1990, there was no significant difference in the number of clutches initiated in any one interval suggesting that re-nesting was frequent, occurred throughout the season, and was as strong as the initial nesting.

Hatching success at re-nests where 53.3% (n = 32) hatched successfully was lower but not significantly different ($t = 1.526$, $P = 0.129$, $df = 139$) from hatching success observed at initial nests where 63.8% (n = 141) hatched successfully. Fledging success was also lower at re-nests (23.1%, n = 52) than at initial nests (30.9%, n = 285) but did not differ significantly ($t = 1.343$, $P = 0.181$, $df = 139$).

Limiting Factors

Piping plovers lost 38.7% (180/465) of all eggs before hatching at Chincoteague NWR from 1989 through 1991. The greatest single cause of eggs loss (Table 1.11) was nest abandonment (52 eggs, n = 3 yrs.) which occurred mostly in 1991 (94.2%) and was largely the result of harassment or predation of the adults by red foxes (Vulpes vulpes) at nests that were otherwise protected by predator exclosures. Flooding

from tidal overwash or from rain was the next leading cause of egg loss (23.9%). Most egg loss from flooding (51.2%) occurred on the Hook in 1990 and resulted mostly from rain pools formed during heavier than normal rainfall in May of that year (Table 1.12, Figure 1.11). Other sources of egg loss were predation by avian predators (18.3%) including fish crows (Corvus ossifragus), boat-tailed grackles (Quiscalus major), and red-winged blackbirds (Agelaius phoeniceus), predation by red foxes (6.7%), predation by raccoons (Procyon lotor)(1.1%), wind-drifted sand (8.3%), and infertile eggs (8.9%). Five eggs (2.8%) were lost to unknown or undetermined causes.

Fish crows were often observed following researchers checking piping plover nests. On one occasion fish crows were observed taking eggs from a piping plover nest within a small colony of least terns (Sterna albifrons). Most often, predators were identified from tracks left at the nest. I could not document any instances of gull predation on piping plover eggs in this study.

Ghost crabs (Oncypoda quadrata) removed eggs from 5 nests, 3 on the Wild Beach and 2 on the Hook, but did not eat them. The eggs were returned to the nest by researchers. On one occasion, ghost crabs burrowed beneath a piping plover nest. One egg subsequently disappeared from the nest but it could not be determined if ghost crabs depredated the egg. There were more nests (n = 19) losing at least one egg in 1991 (Table 1.11) than in any other year but there was no

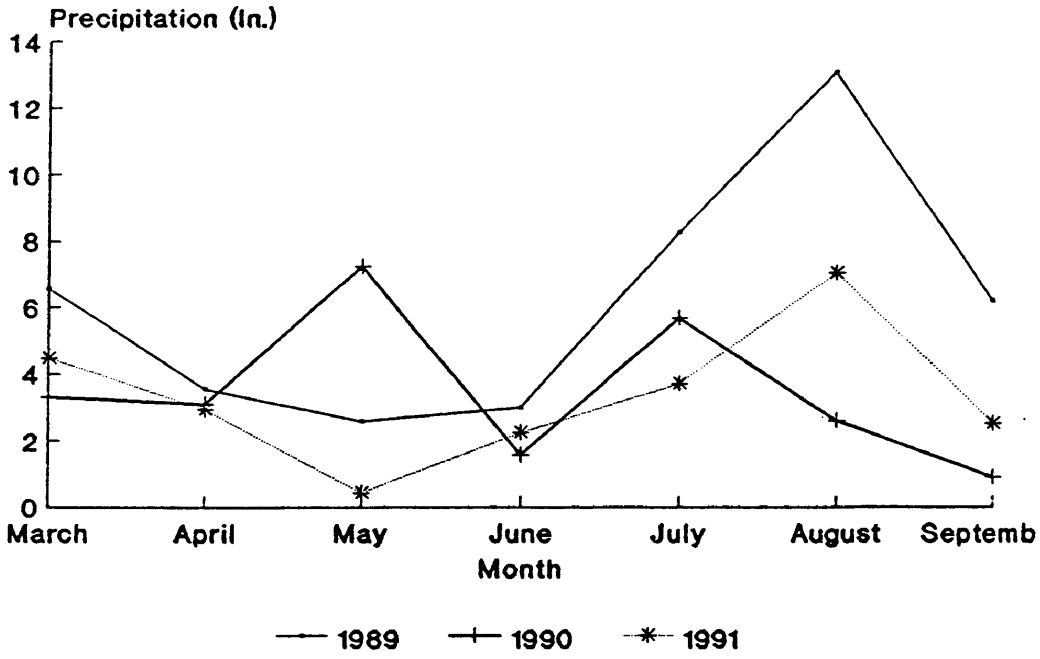
Table 1.11. Causes of egg loss at all piping plover nests at Chincoteague National Wildlife Refuge, Virginia, 1989 - 1991.

				Eggs Lost To:									
Area	Year	Nests (N)	Nests Losing ≥ 1 Egg (%)	AVIAN	FOX	RACCOON	FLOOD	WIND	INFERTILE	ABANDON	UNKNOWN	Total Eggs Lost	Eggs Lost/ Nest
Hook	1989	20	12 (60.0)	8	0	0	1	4	6	0	4	23	1.15
	1990	33	24 (72.7)	20	4	0	22	6	3	0	0	55	1.67
	1991	25	8 (32.0)	2	4	0	0	1	3	15	0	25	1.00
Wild	1989	8	1 (12.5)	0	0	2	0	0	0	0	0	2	0.25
Beach	1990	16	3 (18.8)	0	4	0	6	4	0	0	0	14	0.88
	1991	9	2 (22.2)	0	0	0	0	0	0	7	0	7	0.78
Wash	1989	8	4 (50.0)	0	0	0	7	0	2	0	0	9	1.13
Flats	1990	10	6 (60.0)	0	0	0	7	0	2	3	1	13	1.30
	1991	12	9 (75.0)	5	0	0	0	0	0	27	0	32	2.67
Refuge	1989	36	17 (47.2)	8	0	2	8	4	8	0	4	34	0.94
	1990	59	13 (22.0)	20	8	0	35	10	5	3	1	82	1.39
	1991	46	19 (41.3)	5	4	0	0	1	3	49	0	64	1.39

Table 1.12. Temperature and precipitation at Chincoteague NWR, March through August, 1989 - 1991 (National Oceanic and Atmospheric Administration).

		Temperature (°C)			Precipitation (In.)				
Month	Year	Avg. Max.	Avg. Min.	Avg.	Total	Days w/ > 0.10	Days w/ > 0.50	Days w/ > 1.0	Greatest In 24 Hrs.
March	1989	11.36	2.48	7.26	6.55	12	4	2	1.70
	1990	14.28	4.0	9.17	3.30	9	3	0	0.36
	1991	13.71	3.94	8.82	4.47	7	3	2	1.28
April	1989	14.78	5.96	10.95	3.54	6	3	2	1.21
	1990	17.83	7.06	12.44	3.08	10	1	0	0.50
	1991	19.10	8.61	13.90	2.94	5	2	2	2.26
May	1989	20.01	11.80	16.56	2.85	8	2	0	0.94
	1990	21.72	12.22	17.0	7.23	10	6	3	2.49
	1991	26.60	15.10	20.87	0.43	1	0	0	0.34
June	1989	26.66	19.38	23.71	3.00	10	1	0	0.65
	1990	27.72	17.33	22.56	1.57	2	1	1	1.34
	1991	28.64	17.98	23.31	2.24	4	2	0	0.70
July	1989	29.08	20.90	24.66	8.25	7	3	3	2.88
	1990	30.56	21.22	25.89	5.67	10	4	2	1.26
	1991	30.75	21.50	26.14	3.70	6	2	1	1.64
August	1989	28.91	20.53	24.15	13.07	8	5	3	6.36
	1990	29.11	20.39	24.78	2.60	6	1	1	1.10
	1991	30.03	20.98	25.53	7.02	4	2	2	5.72

Figure 1.11. Total monthly precipitation at Chincoteague NWR, March - September, 1989 - 1991.


Precipitation (In.)
14
12
10
8
6
4
2
0
March
April
May
June
July
August
Septemb
Month
1989
1990
1991

significant difference between years in the number of nests losing one or more eggs ($G = 1.3724$, $P > 0.05$). Eggs were lost at a rate of 1.39 eggs/nest in 1990 and in 1991, higher than in 1989 (0.94 eggs/nest). But there was no statistically significant difference between years in the total number of eggs lost each year ($G = 4.8548$, $P > 0.05$) based on the percentage of nests found per year.

Factors limiting piping plover productivity during brood rearing were more difficult to assess. Chicks frequently disappeared overnight without any indication of the source of loss. I attributed sources of chick loss based on evidence left in the brood-rearing area or by prior knowledge of the most active predators in specific areas.

Losses during brood-rearing were much higher than losses during incubation. A total of 197 chicks (69.1%) failed to reach fledging age (n = 3 yrs.). Most chick loss was attributed to predators, especially red foxes (69/197 chicks, 35.0%). Red foxes maintained active den sites in all three nesting areas and were often sighted during daylight hours. They typically traveled along dune lines where they may have been searching for small mammalian prey and encountering piping plovers in the process.

On the Wild Beach, ghost crabs were indicated as the most frequent predator of piping plover chicks (41/80 chicks, 51.3%). Although I never witnessed predation by ghost crabs, I did frequently observe ghost crab attacks on chicks in the

daytime while piping plover adults defended against the attacks. Ghost crabs were believed to be responsible for 22.8% of all chick loss (45/197 chicks).

Fish crows were observed twice flying away with pre-fledged piping plover chicks and were responsible for 4.6% of all chick loss (9/197 chicks). I frequently (n = 32) observed from 2 - 10 adult piping plovers mobbing fish crows in tern-like fashion as the crows approached incubating or brooding piping plovers.

Gull-billed terns (Sterna nilotica) and laughing gulls (Larus atricilla) were each observed attempting to take pre-fledged piping plover chicks. Gull-billed terns are known to take least tern chicks (Dinsmore 1990). These predators also elicited mobbing behavior from adult piping plovers. No predation of chicks, however, could be attributed to these species.

Severe weather was responsible for chick loss only in 1989 when 16 chicks (9, Hook; 7, Wash Flats) perished in a severe rainstorm on 19 July.

A large percentage of all chick loss (29.4%, 58/197 chicks) occurred without my being able to determine any obvious clues to the cause of the loss.

COLOR BANDING ADULTS AND YOUNG

From 28 April to 24 June 1989, I captured 36 adult piping plovers (16 males, 20 females) on 25 different nests (16, Hook; 4, Wild Beach, 3, Wash Flats). I banded 25 adults with unique color band combinations and USFWS bands (Table 1.13). Eleven adults were already banded from previous studies. One adult male captured on 14 June was missing the right foot and tarsometatarsus. Two color bands were present on the left tarsometatarsus. I removed the color bands and placed a USFWS aluminum band only on the left tarsometatarsus.

No differences could be detected in the mass, wing chord, or culmen length of adult male and female piping plovers (Table 1.14).

Twenty-six pre-fledged piping plover chicks (13, Hook; 5, Wild Beach; 8, Wash Flats) were captured and banded from 3 June to 21 July, 1989 (Table 1.15). One chick, captured at 5 days of age was judged too small for all four bands so only the USFWS aluminum band was applied. The mean age of chicks at banding was 10.1 days, SE = 0.6, range = 5 - 15). Full broods were captured only when they involved 1 or 2 chicks.

The mean size of captured broods was 1.7 chicks, SE = 0.1, range = 1 - 3). Most chicks that were banded in this study (81%, 21/26) were known to survive to fledging age.

A regression of chick weights (Figure 1.12) at time of capture on their age at time of capture showed a strong

Table 1.13. Adult piping plovers banded at Chincoteague National Wildlife Refuge, 1989.

Date	Area	Sex	Color Combination TL/BL/TR/BR	USFWS #
4/28/89	H	F	STR/FWS/WHI/WHI	8001-90523
4/29/89	H	F	STR/FWS/WHI/BLU	8001-90524
5/04/89	H	M	STR/FWS/WHI/RED	8001-90525
5/04/89	WF	F	STR/FWS/WHI/YEL	8001-90526
5/04/89	WF	M	STR/FWS/WHI/GRE	8001-90527
5/09/89	WF	F	STR/FWS/WHI/ORA	8001-90528
5/12/89	H	F	STR/FWS/WHI/BLA	8001-90529
5/15/89	H	M	STR/FWS/BLU/WHI	8001-90530
5/23/89	H	M	STR/FWS/BLU/BLU	8001-90531
5/25/89	H	M	STR/FWS/BLU/RED	8001-90532
5/26/89	H	F	STR/FWS/BLU/YEL	8001-90533
5/26/89	WB	F	STR/FWS/BLU/GRE	8001-90534
5/31/89	WF	F	STR/FWS/BLU/ORA	8001-90535
6/01/89	H	M	STR/FWS/BLU/BLA	8001-90536
6/05/89	H	M	STR/FWS/RED/BLU	8001-90538
6/06/89	H	F	STR/FWS/RED/RED	8001-90539
6/10/89	H	F	STR/FWS/YEL/BLU	8001-90545
6/10/89	H	M	STR/FWS/YEL/RED	8001-90546
6/10/89	WB	F	STR/FWS/YEL/YEL	8001-90547
6/13/89	WB	M	STR/FWS/YEL/ORA	8001-90549
6/14/89	H	F	STR/FWS/YEL/BLA	8001-90550
6/14/89	H	M	- /FWS/ - / -	8001-90551
6/17/89	WF	F	STR/FWS/GRE/GRE	8001-90556
6/22/89	H	M	STR/FWS/GRE/ORA	8001-90559
6/24/89	H	M	STR/FWS/GRE/BLA	8001-90560

Table 1.13 (Continued)

Abbreviation Codes The following abbreviation codes are used throughout the banding tables and will not be repeated in subsequent tables.

Band Positions

TL=top position, left leg
BL=bottom position, left leg
TR=top position, right leg
BR=bottom position, right leg.

Band Colors

BLA = black *
WHI = white *
RED = red *
BLU = blue *
GRE = green *
YEL = yellow *
ORA = orange *
STR = black and white stripe (narrow) *
GRA = gray
LBL = light blue
BWW = black and white stripe (wide)
RF = red flag
BF = black flag
FWS = U.S. Fish and Wildlife Service, Aluminum.

* Used in this study.

Locations

H = Hook
WB = Wild Beach
WF = Wash Flats
AINS = Assateague Island National Seashore, MD
Cobb = Cobb Island, VA
Cedar = Cedar Island, VA
Met = Metompkin Island, VA
CL = Cape Lookout, NC
CH = Cape Hatteras, NC
Oc = Ocracoke Island, NC
FLA = Bahio Hondo, FL

Table 1.14. Morphometrics of breeding piping plovers captured at Chincoteague NWR, 1989.

	Mass (g)			Wing Chord (mm)			Culmen (mm)		
	N	Mean	SE	N	Mean	SE	N	Mean	SE
Male	16	54.49	0.67	16	11.75	0.08	16	12.52	0.20
Female	20	55.65	0.69	20	11.85	0.06	20	12.83	0.10
Probability [1]		P=0.2710			P=0.4725			P=0.1858	

[1] Wilcoxon two-sample Rank Sum test

Table 1.15. Juvenile piping plovers banded at Chincoteague National Wildlife Refuge, 1989. See Table 1.13 for abbreviation codes.

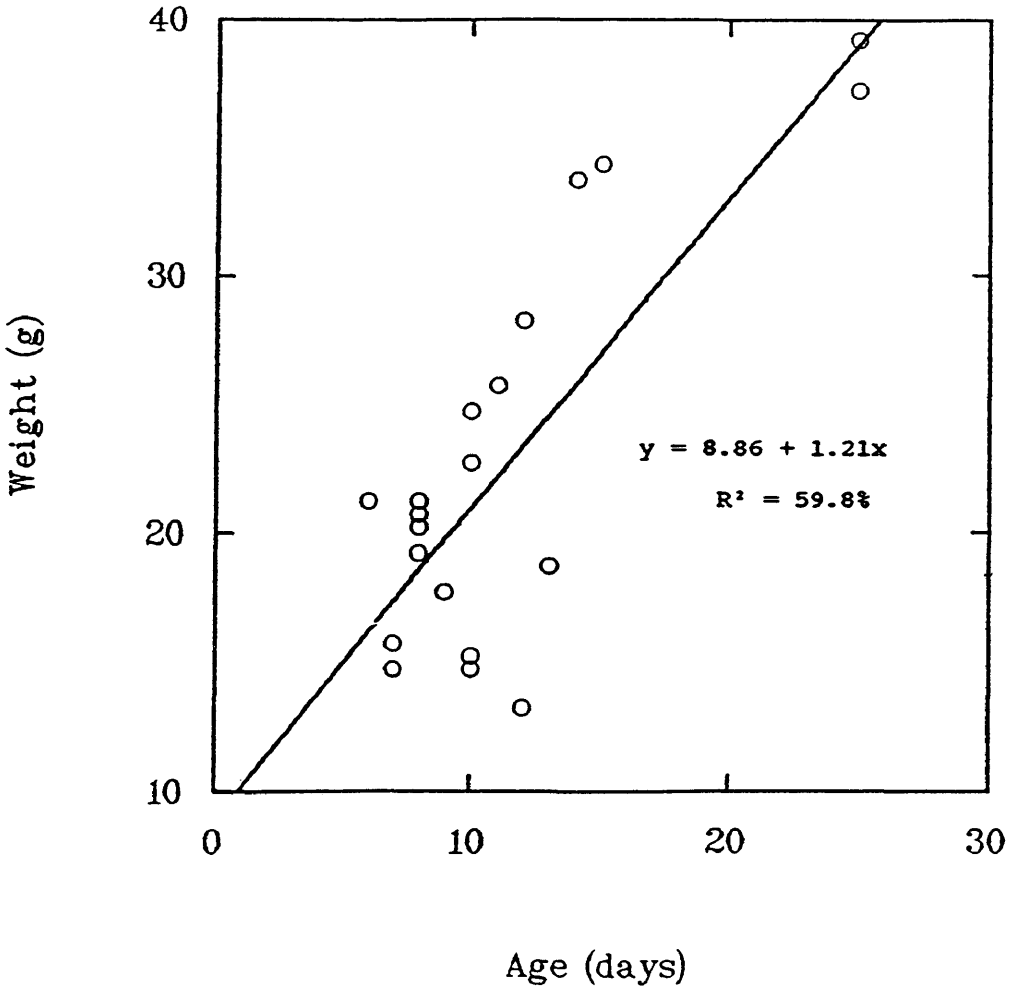
Area	Sex	Age	Color Combination TL/BL/TR/BR	USFWS No.	Brood Size[1]/ Banded[2]	Chick Fate
6/3/89	H	U 10 days	STR/FWS/RED/WHI	8001-90537	4/1	fledged
6/6/89	H	U 10 days	STR/FWS/RED/YEL	8001-90540	3/1	unknown/fledged[3]
6/7/89	H	U 8 days	STR/FWS/RED/GRE	8001-90541	2/2	fledged
6/7/89	WF	U 6 days	STR/FWS/RED/ORA	8001-90542	2/2	fledged
6/8/89	H	U 12 days	STR/FWS/RED/BLA	8001-90543	3/1	fledged
6/10/89	H	U 11 days	STR/FWS/YEL/WHI	8001-90544	2/2	fledged
6/13/89	WF	U 15 days	STR/FWS/YEL/GRE	8001-90548	2/2	fledged
6/14/89	H	U 14 days	STR/FWS/GRE/WHI	8001-90552	2/1	fledged
6/15/89	H	U 8 days	STR/FWS/GRE/BLU	8001-90553	4/3	fledged
6/15/89	H	U 8 days	STR/FWS/GRE/RED	8001-90554	4/3	fledged
6/15/89	H	U 8 days	STR/FWS/GRE/YEL	8001-90555	4/3	fledged
6/21/89	WB	U 5 days**	- /FWS/ - / -	8001-90557	3/2	unknown
6/21/89	WB	U 15 days*	STR/FWS/BLA/WHI	8001-90558	3/2	unknown/fledged[3]
6/28/89	WF	U 12 days*	STR/FWS/ORA/WHI	8001-90561	2/1	fledged
6/28/89	WF	U 10 days*	STR/FWS/ORA/BLU	8001-90562	2/2	fledged
6/28/89	WF	U 10 days*	STR/FWS/ORA/RED	8001-90563	2/2	fledged
6/30/89	WF	U 7 days	STR/FWS/ORA/YEL	8001-90564	3/2	unknown
6/30/89	WF	U 7 days	STR/FWS/ORA/GRE	8001-90565	3/2	fledged
7/1/89	H	U 13 days	STR/FWS/ORA/ORA	8001-90566	2/1	unknown
7/1/89	WB	U 8 days*	STR/FWS/ORA/BLA	8001-90567	2/1	unknown
7/1/89	WB	U 12 days	STR/FWS/BLA/BLU	8001-90568	1/1	fledged

Table 1.15 (Continued). Juvenile piping plovers banded at Chincoteague National Wildlife Refuge, 1989.

Area	Sex	Age	Color Combination TL/BL/TR/BR	USFWS No.	Brood Size[1]/ Banded[2]	Chick Fate
7/5/89	H	U 10 days	STR/FWS/BLA/RED	8001-90569	2/2	fledged
7/5/89	H	U 10 days	STR/FWS/BLA/YEL	8001-90570	2/2	fledged
7/8/89	WB	U 15 days*	STR/FWS/BLA/GRE	8001-90571	2/1	fledged
7/14/89	H	U 10 days	STR/FWS/BLA/ORA	8001-90572	1/1	unknown
7/21/89	WF	U 9 days	STR/FWS/BLA/BLA	8001-90573	1/1	fledged

[1] Brood size on date of banding.
[2] Number of chicks banded from brood.
[3] Observed as AHY in later year. Not listed as fledgling in 1989.
* Hatching date unknown. Age of chick estimated by plumage.
** Hatching date unknown. Age of chick estimated by plumage. Color bands not added due to size and age of chick.

Figure 1.12. Relationship between mass of pre-fledged piping plover chicks and age of same chicks, 1989. ($n = 21$, $y = 8.86 + 1.21x$, $R^2 = 59.8\%$, $P < 0.001$).


40
30
20
10
0
10
20
30
Weight (g)
Age (days)
y = 8.86 + 1.21x
R² = 59.8%

positive relationship. Only chicks of known ages (n = 21) were used in the analysis. A large and significant portion of the variance in weight (R^2 = 59.8%, $P < 0.001$) was explained by the simple regression line suggesting that chicks were finding sufficient nourishment and adding weight consistently throughout the pre-fledging period.

I found that 61% (86/141, total = 3 yrs.) of all nests involved at least one color-banded adult with a complete combination of four bands allowing accurate field identification. This greatly simplified estimates of population size and nesting success.

Adult piping plovers returned in subsequent years at a much greater rate than juveniles in this study (Table 1.16). Eighty-three percent of adults banded in 1989 returned in the following year whereas only 44% of piping plovers banded as chicks in 1989 returned the following year. The difference in return rates between adults and juveniles was significant (X^2 = 8.5067, df = 1, $P < 0.005$). Two years after banding, piping plovers banded as juveniles continued to return at a much lower rate (20%) than those banded as adults (75%). But at two years of age, piping plovers banded as chicks showed no significantly different return rates than those banded two years previously as adults (X^2= 3.4727, df = 1, $P > 0.05$).

Adult piping plovers exhibited strong nesting philopatry to Assateague Island from 1989 to 1991. Fifteen of 24 (62.5%) adult piping plovers color-banded in 1989 returned as breeders

to Chincoteague NWR in 1990 and 13 of 24 (54.2%) returned again as breeders in 1991 (Table 1.17). Juveniles returned as breeders at a much lower rate in 1990 (6/25, 24%)(Table 1.18). None returned as breeders in 1991 although two were observed as breeders on Cobb Island (R. Beck, pers. comm.) and Cedar Island, Virginia (pers. observ.).

Sixty-seven color banded piping plovers were observed at Chincoteague NWR from 1989 to 1991 that had color combinations other than those used in this study. The dates of their first and last sightings and their nesting status are given in Table 1.19 and their banding histories are given in Table 1.20. Twenty-five of these (37.3%) were observed as breeders at Chincoteague NWR in one or more years. Twenty-nine (43.3%) were banded at locations other than Chincoteague NWR.

PIPING PLOVER LEG INJURIES

I observed a total of 14 different piping plovers with various leg injuries at Chincoteague NWR from 1989 to 1991 (Table 1.21). Of these, 4 leg injuries (28.6%) could be confirmed by color band combinations as birds banded in this study. No leg injuries were observed on birds that were not banded. Injuries ranged in severity from apparent limping to complete loss of the leg.

Some piping plovers with injuries to their legs (9/14, 64%) continued to breed despite the injury. I trapped one male with a severed right leg, while he was incubating

Table 1.16. Piping plovers color banded at Chincoteague NWR in 1989 and the number observed alive in 1990, 1991.

Population	No. Banded (1989)	No. Observed Alive	
		1 yr.(%)	2 yr.(%)
CNWR adults	24	20 (83.3)	18 (75.0)
CNWR chicks	25	11 (44.0)	5 (20.0)
X^2		8.5067	3.4727
Probability		$P < 0.005$	$P > 0.05$

Table 1.17. Resightings of piping plovers banded as adults at Chincoteague National Wildlife Refuge, 1989. See Table 1.13 for abbreviation codes.

Date	Area	Sex	Color Combination TL/BL/TR/BR	USFWS #	Resighted 1990			Resighted 1991		
					Dates	Location-Nesting [1]		Dates	Location-Nesting [1]	
4/28/89	H	F	STR/FWS/WHI/WHI	8001-90523	4/25-6/24	H	Yes	3/21	H	Yes
4/29/89	H	F	STR/FWS/WHI/BLU	8001-90524	6/07-8/05	H	Yes	4/08-7/14	WB	Yes
5/4/89	H	M	STR/FWS/WHI/RED	8001-90525	6/20-8/05	H	Yes	3/25-8/05	H	Yes
5/4/89	WF	F	STR/FWS/WHI/YEL	8001-90526	3/30-7/28	WF	Yes	4/01-6/18	WF	Yes-C
5/4/89	WF	M	STR/FWS/WHI/GRE	8001-90527	4/10-7/29	WF	Yes-A	3/06-7/16	WF	Yes-B
					7/16	AINS	No			
5/9/89	WF	F	STR/FWS/WHI/ORA	8001-90528	5/06-7/05	H	Yes-D	3/15	H	No
5/12/89	H	F	STR/FWS/WHI/BLA	8001-90529	4/05	H	No	4/03-7/11	H	Yes
5/15/89	H	M	STR/FWS/BLU/WHI	8001-90530	3/22-7/05	H	Yes-D	none [2]		
5/23/89	H	M	STR/FWS/BLU/BLU	8001-90531	4/20/90	H	No	3/26-4/01	H	No
5/25/89	H	M	STR/FWS/BLU/RED	8001-90532	3/27-7/21	H	Yes-C	3/20-7/14	H,WF	Yes-A
5/26/89	H	F	STR/FWS/BLU/YEL	8001-90533	3/27-7/21	H	Yes-C	3/17-6/20	H,WF	Yes-A
5/26/89	WB	F	STR/FWS/BLU/GRE	8001-90534	none			none		
5/31/89	WF	F	STR/FWS/BLU/ORA	8001-90535	4/10-7/28	WF	Yes-A	3/25-6/21	WF	Yes-B
6/1/89	H	M	STR/FWS/BLU/BLA	8001-90536	5/06	H	Yes	3/06-6/25	H	Yes
6/5/89	H	M	STR/FWS/RED/BLU	8001-90538	6/14-8/04	H	Yes	3/27,7/19	H	No
6/6/89	H	F	STR/FWS/RED/RED	8001-90539	4/20-5/11	H	Yes	3/25-7/16	H	Yes
6/10/89	H	F	STR/FWS/YEL/BLU	8001-90545	none			7/18	H	No
6/10/89	H	M	STR/FWS/YEL/RED	8001-90546	7/24	WB	No	none		
6/10/89	WB	F	STR/FWS/YEL/YEL	8001-90547	none			none		
6/13/89	WB	M	STR/FWS/YEL/ORA	8001-90549	3/26-7/25	WB,WF	Yes-B	4/01-6/18	WF	Yes-C
6/14/89	H	F	STR/FWS/YEL/BLA	8001-90550	5/01-7/25	WB,WF	Yes-B	none		
6/14/89	H	M	- /FWS/ - / -	8001-90551	none			none		
6/17/89	WF	F	STR/FWS/GRE/GRE	8001-90556	6/30	H	No	none		
6/22/89	H	M	STR/FWS/GRE/ORA	8001-90559	none			3/25-7/14	H	Yes
6/24/89	H	M	STR/FWS/GRE/BLA	8001-90560	none			3/17	H	No

[1] Matching letters following yes indicates a mated pair.
[2] Bird not observed in this year.

Table 1.18. Resightings of piping plovers banded as juveniles at Chincoteague National Wildlife Refuge, 1989. See Table 1.13 for abbreviation codes.

Date	Area	Color Combination TL/BL/TR/BR	USFWS	Resighted 1990 Dates	Location	Nesting	Resighted 1991 Dates	Location	Nesting
6/03/89	H	STR/FWS/RED/WHI	8001-90537	7/21	H	No	5/30,7/18	Cobb Is.	Yes[1]
6/06/89	H	STR/FWS/RED/YEL	8001-90540	4/20-7/27	WF	Yes	4/1,4/2	WF	No
6/07/89	H	STR/FWS/RED/GRE	8001-90541	none[2]			none		
6/07/89	WF	STR/FWS/RED/ORA	8001-90542	none			none		
6/08/89	H	STR/FWS/RED/BLA	8001-90543	6/05-7/02	H	Yes	3/25-4/29	WB, H	No
6/10/89	H	STR/FWS/YEL/WHI	8001-90544	none			none		
6/13/89	WF	STR/FWS/YEL/GRE	8001-90548	6/24-8/01	WB	Yes	5/01	Cedar Is.	Yes
6/14/89	H	STR/FWS/GRE/WHI	8001-90552	3/15	H	No	none		
6/15/89	H	STR/FWS/GRE/BLU	8001-90553	none			none		
6/15/89	H	STR/FWS/GRE/RED	8001-90554	none			4/10	H	No
6/15/89	H	STR/FWS/GRE/YEL	8001-90555	4/10	H	No	none		
6/21/89	WB	- /FWS/ - / -	8001-90557	none			none		
6/21/89	WB	STR/FWS/BLA/WHI	8001-90558	6/16-8/04	H	Yes	none		
6/28/89	WF	STR/FWS/ORA/WHI	8001-90561	none			none		
6/28/89	WF	STR/FWS/ORA/BLU	8001-90562	none			none		
6/28/89	WF	STR/FWS/ORA/RED	8001-90563	none			none		
6/30/89	WF	STR/FWS/ORA/YEL	8001-90564	none			none		
6/30/89	WF	STR/FWS/ORA/GRE	8001-90565	none			none		
7/01/89	H	STR/FWS/ORA/ORA	8001-90566	none			none		
7/01/89	WB	STR/FWS/ORA/BLA	8001-90567	none			none		
7/01/89	WB	STR/FWS/BLA/BLU	8001-90568	none			none		
7/05/89	H	STR/FWS/BLA/RED	8001-90569	5/18	WF	Yes	none		
7/05/89	H	STR/FWS/BLA/YEL	8001-90570	none			none		
7/08/89	WB	STR/FWS/BLA/GRE	8001-90571	5/18-7/23	AINS	Yes	none		
7/14/89	H	STR/FWS/BLA/ORA	8001-90572	none			none		
7/21/89	WF	STR/FWS/BLA/BLA	8001-90573	7/21	H	No	none		

[1] R. Beck, Pers. Comm.
[2] Bird not observed in this year.

Table 1.19. Observations of color-banded piping plovers banded prior to 1989 or from locations away from Chincoteague National Wildlife Refuge. See Table 1.13 for abbreviation codes.

Color Combination		1989			1990			1991		
TL/BL/TR/BR	USFWS	Dates	Loc.	Nest	Dates	Loc.	Nest	Dates	Loc.	Nest
FWS/BLA/ RF/RED	8001-90520	4/1-7/08	H	Yes	none [1]			4/3,7/1	H	No
FWS/WHI/ RF RED	8001-90514	5/04-5/29	H	Yes	3/20-7/07	H	Yes	3/20-8/5	H	Yes
		8/13	CL [2]	No						
		8/13	Oc [4]	No						
FWS/GRE/ RF/RED	8001-90518	5/04-6/27	H	Yes	3/22-7/25	H	No	4/22	WB	No
FWS/BLA/ RF/BLA	871 -62506	5/04-6/14	H	Yes	4/12	H	No	3/17	H	No
BLA/BLA/ RF/FWS	8001-90305	3/28-6/02	H	Yes	5/15	H	Yes	none		
BLU/RED/ RF/FWS	8001-90309	5/17-8/08	H	Yes	4/6-8/4	WB	Yes	none		
FWS/YEL/ RF/RED	8001-90517	3/29-7/18	H	Yes	3/27-8/04	H	Yes	3/19-7/14	H	No
BLA/FWS/ RF/BLA	8001-90560	6/17-7/14	H	Yes	none			none		
BLU/BLU/ RF/FWS	8001-90303	3/29-6/24	H	Yes	3/22-8/14	WF	Yes	3/27-7/13	WB	Yes
FWS/RED/ RF/WHI*	8001-90502	6/10-7/14	H	Yes	none			7/9-7/11	WF,H	No
BLA/FWS/ RF/YEL	8001-90363	6/08-8/17	H	Yes	none			none		
		4/20	CH [2]	No						
FWS/BLA/ RF/BLU	8001-90513	3/28-6/13	WB	Yes	3/26-6/26	H	Yes	6/15	WB	No
FWS/ORA/ RF/RED	8001-90519	3/27-7/08	WB	Yes	3/15-7/03	WB	Yes	5/11	H	No
FWS/BLA/ RF/WHI	8001-90508	4/12-6/15	WB	Yes	none			3/28,5/27	WB	No
BLU/BLA/ RF/FWS		3/16	H	No	3/19-5/21	WB	No	none		
FWS/GRE/ RF/WHI	8001-90504	3/16	H	No	none			5/17	H	Yes
FWS/ORA/ RF/BLA	8001-90338	3/20	H	No	3/20-9/5	WB	Yes	4/2,6/8	WF	No
		10/15	FL [2]	No						
FWS/WHI/ RF/ORA	8001-90357	3/20	H	No	3/27	H	No	5/11	H	No
FWS/RED/GRE/GRA		3/27	WB	No	none			none		
BF /FWS/GRE/YEL	981 -39580	3/27	WB	No	none			none		
BF / - /YEL/FWS	981 -39596	4/26	WB	No	none			none		
BLA/GRE/ RF/FWS	8001-90325	3/27	H	No	none			none		
WHI/FWS/ RF/YEL	8001-90334	3/28	WB	No	none			none		

Table 1.19 (Continued)

Color Combination TL/BL/TR/BR	USFWS	1989 Dates	1989 Loc.	1989 Nest	1990 Dates	1990 Loc.	1990 Nest	1991 Dates	1991 Loc.	1991 Nest
GRE/YEL/ RF/FWS	8001-90308	3/29	WB	No	none			none		
FWS/RED/ RF/RED	8001-90516	3/31	WB	No	3/26-7/21	H	Yes	3/25-79	H	No
FWS/BLU/ RF/WHI	8001-90501	3/31-5/31	WB,H	Yes	3/26-7/31	WB	Yes	3/15-5/10	WB	Yes
		8/13-8/29	CL [5]	No						
FWS/BLU/ RF/RED	8001-90515	4/3	H	No	3/22-6/16	H	Yes	none		
BLA/ BW/ BF/FWS		4/4	WB	No	none			none		
FWS/BLU/ RF/BLU	8001-90507	4/7	WB	No	none			none		
RF /FWS/BLA/RED	8001-90443	4/27	H	No	none			none		
RF /FWS/RED/BLU	8001-90426	5/2	WF	No	5/25	Met.	Yes [3]	none		
RED/RED/ RF/FWS	8001-90301	9/11	H	No	3/27	H	No	5/18	H	Yes
RF /FWS/YEL/YEL	8001-90500	9/13	H	No	none			none		
WHI/FWS/BWW/YEL	8001-90334	7/5,8/1	H	No	none			none		
FWS/ORA/ RF/BLU	8001-90511	8/4	H	No	3/26-4/27	WB	No	none		
FWS/ORA/ RF/WHI	8001-90504	7/12,7/25	H	No	4/22-7/24	H	Yes	5/5-6/18	H	Yes
BLU/FWS/ RF/BLA		6/21	H	No	none			none		
FWS/WHI/ RF/YEL		7/6	H	No	3/21-7/31	H	Yes	3/28-7/20	H	Yes
RF /FWS/GRE/BLU	8001-90433	6/29	H	No	none			none		
		3/27	CL [5]	No						
RF /FWS/WHI/ORA	8001-90421	6/28	H	No	none			none		
BLA/FWS/ RF/BLA		6/28	H	No	none			none		
WHI/FWS/ RF/BLA		7/4	H	No	none			none		
BF /FWS/LBL/ORA	871 -75282	7/19	H	No	none			none		
RF /FWS/RED/RED	9001-90409	5/18	H	No	none			none		
- / - / - /FWS	871 -62493	4/29	H	Yes	none			none		
BLA/FWS/ RF/BLU	1392-12609	7/5	H	No	none			none		
GRE/FWS/ RF/BLU	1391-12610	6/16	H	No	none			none		
BLA/BLA/ RF/FWS	8001-90305	3/28	H	No	none			none		

Table 1.19 (Continued)

Color Combination TL/BL/TR/BR	USFWS	1989 Dates	1989 Loc.	1989 Nest	1990 Dates	1990 Loc.	1990 Nest	1991 Dates	1991 Loc.	1991 Nest
FWS/GRE/YEL/ORA		none			3/14	H	No	none		
YEL/FWS/BWW/WHI	8001-90335	none			3/25-8/10	H	Yes	5/15-6/21	H	Yes
WHI/FWS/ RF/RED	8001-90355	none			4/29-5/07	H	Yes	none		
FWS/GRE/ RF/ORA	8001-90333	none			3/23	H	No	none		
ORG/BLA/BWW/FWS		none			8/4	H	No	none		
YEL/FWS/BWW/RED	8001-90344	none			6/15	H	No	none		
BLU/BLU/BWW/FWS	8001-90374	none			6/6	H	No	none		
RED/BLA/ RF/FWS		none			4/20	H	No	none		
BLA/RED/ RF/FWS	8001-90326	none			7/27	H	No	none		
RF /FWS/ORA/GRE	8001-90438	none			7/12	H	No	none		
FWS/BLU/ RF/BLA	8001-90354	none			none			3/17-8/24	H	No
FWS/WHI/WHI/ RF		none			none			3/26	H	No
FWS/YEL/ RF/WHI	8001-90503	none			7/21	H	No	4/1-4/8	H	No
FWS/WHI/ RF/ORA	8001-90357	none			3/27	H	No	5/11	H	No
WHI/FWS/ RF/WHI	8001-90345	none			none			7/24	H	No
FWS/WHI/ RF/BLA	1391-12602	none			none			7/24	H	No
RED/WHI/ RF/FWS	8001-90312	none			none			5/28-7/9	H	Yes
RED/YEL/BWW/FWS	8001-90384	none			none			5/19	WF	No

1 Bird was not observed in this year.
2 Reported by S. Haig.
3 B.D. Watts and C. Rosenburg.
4 (Wrenn, S.D. 1990)
5 (Coutu, S.D., Fraser, J.D., McConnaughey J.L., and J.P. Loegering. 1990)
* This female was observed with four eggs on Assateague National Seashore, Maryland on 19 May 1989. The eggs hatched on 25 May. All four chicks were lost (fox) on 2 June (J. Loegering, Pers. Commun.). Nest at CNWR is a re-nest. Three chicks hatched, but did not survive.

Table 1.20. Banding histories of color-banded piping plovers observed in this study but banded prior to 1989 or at locations away from Chincoteague National Wildlife Refuge. See Table 1.13 for abbreviation codes.

Color Combination TL/BL/TR/BR	USFWS	Banding Year	Age [1]	Banding Location	Bander
FWS/BLA/ RF/RED	8001-90520	1988	AHY	Hook	I. Ailes
FWS/WHI/ RF RED	8001-90514	1988	AHY	Hook	I. Ailes
FWS/GRE/ RF/RED	8001-90518	1988	AHY	Hook	I. Ailes
FWS/BLA/ RF/BLA	871 -62506	1987	AHY	Hook	M. Patterson
BLA/BLA/ RF/FWS	8001-90305	1987	AHY	Wash Flats	M. Patterson
BLU/RED/ RF/FWS	8001-90309	1987	AHY	Wash Flats	M. Patterson
FWS/YEL/ RF/RED	8001-90517	1988	AHY	Hook	I. Ailes
BLA/FWS/ RF/BLA	871 -62506	1987	AHY	Hook	M. Patterson
BLU/BLU/ RF/FWS	8001-90303	1988	AHY	Wash Flats	I. Ailes
FWS/RED/ RF/WHI	8001-90502	1988	AHY	Wash Flats	I. Ailes
BLA/FWS/ RF/YEL	8001-90363	1988	AHY	AINS	M. Patterson
FWS/BLA/ RF/BLU	8001-90513	1988	AHY	Wild Beach	I. Ailes
FWS/ORA/ RF/RED	8001-90519	1988	AHY	Hook	I. Ailes
FWS/BLA/ RF/WHI	8001-90508	1988	AHY	Wild Beach	I. Ailes
FWS/GRE/ RF/WHI	8001-90504	1988	AHY	Hook	I. Ailes
FWS/ORA/ RF/BLA	8001-90338	1988	AHY	AINS	M. Patterson
FWS/WHI/ RF/ORA	8001-90357	1988	AHY	AINS	M. Patterson
FWS/RED/GRE/GRA	?				
BF /FWS/GRE/YEL	981 -39580	1988	AHY	Sandwich, MA	E. Strauss
BF / - /YEL/FWS	981 -39596	1988	AHY	Centerville, MA	E. Strauss
BLA/GRE/ RF/FWS	8001-90325	1987	AHY	AINS	M. Patterson
WHI/FWS/ RF/YEL	8001-90334	1988	AHY	AINs	M. Patterson
GRE/YEL/ RF/FWS	8001-90308	1987	AHY	Wash Flats	M. Patterson
FWS/RED/ RF/RED	8001-90516	1988	AHY	Wild Beach	I. Ailes
FWS/BLU/ RF/WHI	8001-90501	1988	AHY	Wild Beach	I. Ailes
FWS/BLU/ RF/RED	8001-90515	1988	AHY	Wild Beach	I. Ailes

Table 1.20. (Continued)

Color Combination TL/BL/TR/BR	USFWS	Year Banded	Age	Location	Bander
FWS/BLU/ RF/BLU	8001-90507	1988	AHY	Wild Beach	I. Ailes
RF /FWS/BLA/RED	8001-90443	1988	HY	Metompkin Is., VA	R. Cross
RF /FWS/RED/BLU	8001-90426	1988	AHY	Metompkin Is., VA	R. Cross
RED/RED/ RF/FWS	8001-90301	1987	AHY	Wash Flats	M. Patterson
RF /FWS/YEL/YEL	8001-90500	1987	AHY	Metompkin Is., VA	R. Cross
WHI/FWS/BWW/YEL	8001-90334	1988	AHY	AINS	M. Patterson
FWS/ORA/ RF/BLU	8001-90511	1988	AHY	Hook	I. Ailes
FWS/ORA/ RF/WHI	8001-90504	1988	AHY	Hook	I. Ailes
BLU/FWS/ RF/BLA	?				
FWS/WHI/ RF/YEL	?				
RF /FWS/GRE/BLU	8001-90433	1988	AHY	Metompkin Is., VA	R. Cross
RF /FWS/WHI/ORA	8001-90421	1988	AHY	Metompkin Is., VA	R. Cross
BLA/FWS/ RF/BLA	?				
WHI/FWS/ RF/BLA	?				
BF /FWS/LBL/ORA	871 -75282	1987	HY	Monomoy NWR, MA	L. MacIvor
RF /FWS/RED/RED	9001-90409	1987	AHY	Cedar Sandbar, VA	R. Cross
- / - / - /FWS	871 -62493	1988	AHY	Wash Flats	I. Ailes
FWS/GRE/YEL/ORA	?				
YEL/FWS/BWW/WHI	8001-90335	1988	AHY	AINS	M. Patterson [2]
WHI/FWS/ RF/RED	8001-90355	1988	AHY	AINS	M. Patterson
FWS/GRE/ RF/ORA	8001-90333	1988	AHY	AINS	M. Patterson
FWS/BLU/ RF/WHI	8001-90501	1988	AHY	Wild Beach	I. Ailes
ORG/BLA/BWW/FWS	?				
BLA/FWS/ RF/BLU	1391-12609	1988	HY	AINS	M. Patterson
GRE/FWS/ RF/BLU	1391-12610	1988	HY	AINS	M. Patterson
BLU/BLA/ RF/FWS	8001-90303	1987	AHY	Wild Beach	M. Patterson
BLA/BLA/ RF/FWS	8001-90305	1987	AHY	Wash Flats	M. Patterson
YEL/FWS/BWW/RED	8001-90344	1988	AHY	AINS	M. Patterson

Table 1.20. (Continued)

Color Combination TL/BL/TR/BR	USFWS	Year Banded	Age	Location	Bander
BLU/BLU/BWW/FWS	8001-90374	1989	AHY	AINS	J. Loegering
RED/BLA/ RF/FWS	?				
BLA/RED/ RF/FWS	8001-90326	1987	AHY	Hook	M. Patterson
RF /FWS/ORA/GRE	8001-90438	1988	HY	Metompkin Is., VA	R. Cross
FWS/BLU/ RF/BLA	8001-90354	1988	AHY	AINS	M. Patterson
FWS/WHI/WHI/ RF	?				
FWS/YEL/ RF/WHI	8001-90503	1988	AHY	Wild Beach	I. Ailes
FWS/WHI/ RF/ORA	8001-90357	1988	AHY	AINS	M. Patterson
WHI/FWS/ RF/WHI	8001-90345	1988	AHY	AINS	M. Patterson
FWS/WHI/ RF/BLA	1391-12602	1988	HY	AINS	M. Patterson
RED/WHI/ RF/FWS	8001-90312	1987	AHY	AINS	M. Patterson
RED/YEL/BWW/FWS	8001-90384	1989	AHY	AINS	J. Loegering

[1] Age when banded.
[2] Red flag was replaced with black & white striped band (wide) in 1989 by J. Loegering.
? Not a known color combination. Bands were likely mis-read in the field.

Table 1.21. Observations of color banded piping plovers with leg injuries at Chincoteague NWR, 1989 - 1991. See Table 1.13 for abbreviation codes.

Date	Location	Color Combination TL/BL/TR/BR	Breeder	Description of Injury
1989				
3/22/89	WB	- / - /BLA/FWS	no	Left foot missing. Left leg discolored, necrotic.
3/27/89	WB	BLA/FWS/ - / -	no	Right leg missing.
6/14/89	Hook	- /WHI/ RF/ -	yes	Right foot missing. RF position maintained by swollen stump. Tarso-metatarsus swollen 2x normal size.
1990				
3/14/90	Hook	YEL/FWS/ - / -	no	Right foot missing. Swollen stump remains.
3/27/90	Hook	- / - / RF/FWS	no	Left foot missing.
4/12/90	Hook	FWS/BLA/ RF/BLA	yes	Right leg broken, dangling. Hopping on left leg.
4/16/90	Hook	STR/ - /RED/BLU [1]	yes	Left foot missing. Swollen stump present holding band in place.
5/28/90	Hook	STR/FWS/BLU/YEL [1]	yes	Limping. Favoring left leg. Hopping on right leg.
6/09/90	Hook	- /FWS/ - / -	yes	Right foot missing.
6/22/90	Hook	RED/RED/ RF/FWS	yes	Right leg dangling. Hopping on left leg.
7/18/90	Hook	STR/FWS/BLA/WHI [1]	yes	left foot missing.
7/25/90	Hook	STR/ - /BLU/BLA [1]	yes	left foot missing.

Table 1.21 (Continued)

Date	Location	Color Combination TL/BL/TR/BR	Breeder	Description of Injury
1991				
3/27/91	Hook	RED/RED/ RF/ - [2]	no	Right foot missing. Swollen stump remains.
3/27/91	Hook	STR/ - /RED/BLU [1,2]	no	Left foot missing.
4/03/91	Hook	- /FWS/BLU/ -	no	Left foot missing.
4/23/91	WF	STR/FWS/BLU/YEL [1,2]	yes	Left foot missing.
5/09/91	Hook	- /FWS/ - / -	yes	Right foot missing.
7/14/91	Hook	- /FWS/ RF/BLA [2]	yes	Left foot missing.

[1] Color bands added in this study.
[2] Bird observed with leg injury in previous year.

eggs. In addition, 4 of 9 piping plovers (44%) observed with leg injuries in 1990 returned to Chincoteague NWR in the following year.

Leg injuries involving color banded piping plovers were first observed at Chincoteague NWR in 1988 (I. Ailes pers. comm.) when a single bird was found with an injury to the right leg just below the red "flag". Leg injuries were more commonly observed in piping plovers at many Atlantic coast sites and along the Platte River, Nebraska by many observers by 1989.

Although it appears likely that piping plover leg injuries are associated with banding, there does not appear to be any one banding technique that causes the injuries. Injuries were reported across a wide range of band types and application methods among different banders. From this study, however, band related injuries appear to be associated with the use of "flags" or possibly striped bands which were made from a different material than solid colored bands. Of 13 injured piping plovers where the "flag" or striped band position could be determined, 11 (85%) leg injuries occurred to the leg with the "flag" or striped band. Leg injuries may be fundamentally related to banding in piping plovers despite different techniques, due to a build up of mud and sand beneath the bands causing restriction of normal blood circulation. Soft substrates used by piping plovers as foraging sites may contribute to band-related leg injuries.

Due to the frequency of leg injuries observed in piping plovers and also to similar reports in snowy plovers (Charadrius alexandrinus) the U.S. Fish and Wildlife Service recommended a moratorium on banding of piping plovers in 1989. A continuation of the banding moratorium is in order until the cause(s) of leg injuries can be satisfactorily determined and corrected.

DISCUSSION

Breeding population estimates for piping plovers at Chincoteague NWR have varied from 16 - 18 pairs in 1985 (USFWS 1985) to 46 pairs in 1987 (Patterson 1988). The breeding population remained relatively stable during this study (32 - 42 pairs) and may represent an equilibrium between saturation of optimal nesting habitats and low population recruitment due to consistently depressed reproductive success.

Loegering (1992) suggested that there was some natural fluctuation in piping plover populations on Assateague Island in Maryland. That would appear to apply to Chincoteague NWR as well. During the time of this study, the piping plover population in Virginia increased by 27.8% over 1988 figures (Virginia Department of Game and Inland Fisheries 1988) but the increase was largely due to population growth on Metompkin Island (+72% from 1988 to 1989) not to changes on Assateague Island.

Burger and Jenkins (1987) state that low reproductive success reported in many studies of piping plover breeding biology may reflect decreases in optimal habitat, increases in human disturbance, and increases in predators on barrier islands. The detrimental effects of human disturbance have been mitigated at Chincoteague NWR since beach closures were instigated in 1988 (USFWS 1988c). Continuing low reproductive success for piping plovers, then, would seem the result of the availability of optimal habitat and increasing predator pressure.

The Hook remains the most heavily used nesting area by piping plovers at Chincoteague NWR. Patterson (1988) found 35% of all piping plovers at Chincoteague NWR nesting on the Hook. In this study, a mean of 56% (SE = 1.9, n = 3 yrs.) of all piping plovers were found nesting on the Hook.

I found that more piping plovers used the Wild Beach (mean = 25%, SE = 2.8, total = 3 yrs.) as a nesting area than used the Wash Flats (mean = 19%, SE = 2.7, total = 3 yrs.) but much of the Wild Beach (approx. 5 km) remained unused even though it appeared to be suitable nesting habitat. Gaines and Ryan (1988) noted the availability of apparently adequate but unoccupied habitat at several of their study sites in North Dakota. Piping plovers on the Wild Beach may face greater predator pressure if the influx of mammalian predators on the refuge is from the north as the island topography would suggest. Nest site selection on the Wild Beach may be

influenced further by ghost crabs and by a lack of back-dune foraging/brood-rearing habitats such as tidal pools and barrier flats.

During this study, piping plovers arrived at Chincoteague NWR usually in the first week of March, earlier by at least a week than reported by Patterson (1988) on Assateague Island. MacIvor (1990) found piping plovers in mid-March in Massachusetts and Wilcox (1959) reported piping plovers were observed on Long Island by the last week in March. I typically observed piping plovers first on the Wild Beach although most nesting occurred on the Hook suggesting that some early observations of piping plovers may have been transient birds enroute to more northern breeding grounds. Observations of color-banded piping plovers from Massachusetts in the early spring lend support to this hypothesis. MacIvor (1988) noted that some piping plovers may go undetected in the early spring due to differences in the number of observation days and survey effort between studies.

Breeding site fidelity for piping plovers has been reported as high as 92% (Haig and Oring 1987b) in Minnesota and as low as 15% (Cairns 1977) in Nova Scotia. I found that 83% (20/24) of adult piping plovers that I color banded in 1989 returned to the refuge in the following year (Table 1.16). My return rate for adults is in close agreement with the return rate found in Massachusetts (74%, Melvin et al. 1991). Of those returning adults, 79% (15/19) returned and

bred. Previous experience in an area may provide advantages to returning birds in acquiring food, territories, and mates (Haig and Oring 1988b). The proportion of males returning (75%, 9/12) was similar to the proportion of females returning (77%, 10/13) in this study. Haig and Oring (1988b) found no significant difference in male and female return patterns.

Juvenile return rates were lower than adults. Only 44% (11/25) piping plovers banded as chicks in 1989 returned to Chincoteague NWR the following year. Of all juveniles banded, 24% (6/25) returned and bred in their first year. Juvenile return rates range from 5% in New York (Wilcox 1959) to 41% in Maryland (Loegering 1992) where 28% returned to breed. Dispersal patterns of juveniles are poorly understood. In 1991, I found two piping plovers, banded as chicks in our study, breeding on other barrier islands in Virginia (Cobb Island, Cedar Island)(Table 1.18). Haig (1987) reported a piping plover chick from Manitoba discovered at Long Point, Ontario at one year of age. Loegering (1992) suggests that dispersal to other breeding sites could affect estimates of survival rates. Root et al. (1992), however, observed only three (0.8%) piping plovers at sites away from their North Dakota banding site in subsequent years and suggest that emigration of plovers from their study site was relatively unimportant in determining survival rates.

Foraging was the most common behavior that piping plovers were engaged in during the first month after arrival at

Chincoteague NWR. Foraging occurred most often in the surf zone on the Wild Beach but shifted from the surf zone to areas away from the surf zone between early (< 1 May) and late (≥ 1 May) season on the Hook. The reasons for the observed shift in foraging site preference on the Hook are uncertain but it may be due to an early depletion of invertebrate prey in the surf zone after heavy use of those areas by other migrating shorebirds. Alternatively, piping plovers may be shifting foraging sites to allow more attention to courtship and incubation duties associated with the nesting territory.

Another possibility is that prey are not readily available to piping plovers at sites away from the surf zone until later in the season due to climactic factors. Climactic factors may influence foraging behavior by effecting prey availability, especially since more insect prey are present at sites away from the surf zone (Loegering 1992). Many studies (King and Farner 1974, Pienkowski 1982, 1983, and others) have emphasized the importance of climactic factors and other physical environmental conditions on prey availability and subsequently on feeding behavior of shorebirds. If piping plovers forage optimally (Krebs and McCleery 1984), they will continue to forage in those habitats that offer the most profitable prey. There may be a temporal/seasonal shift in the availability of prey in the surf zone and at sites away from the surf zone on the Hook which is not realized on the Wild Beach or the shift in foraging sites on the Wild Beach may be

to areas away from the Wild Beach altogether. From my observations, both oceanside foraging areas and alternative foraging areas are important to piping plovers during the breeding season at Chincoteague NWR.

Piping plovers are visual foragers, using a run and peck method to capture prey (Cairns 1977, Pienkowski 1983a). Beckerman (1988) reported that piping plovers captured prey at a rate 3 times greater in the wash zone than they did on the upper, gravel beach in North Dakota. At Brigantine Beach in New Jersey, Burger (1988) found that piping plovers generally rest in the dunes and feed along the ocean or inlets. Some authors (Burger 1988, Cairns 1977, Whyte 1985) have noted that chicks fed on the upper beach more often than adults did. At study sites in Saskatchewan, 70% of piping plover foraging occurred within 5 M of the water's edge (Whyte 1985) and in Michigan piping plovers maintained the intensity of shoreline foraging throughout the season (Brown 1987).

The intensity of shoreline foraging may be dependent upon the availability of alternative foraging sites at Chincoteague NWR. Piping plovers on the Wild Beach were rarely observed foraging at sites away from the shoreline, but may have travelled greater distances to the Wash Flats or to tidal mudflats to locate prey when it was not available in the surf zone. Patterson (1988) often observed piping plovers flying between the Wild Beach and the Wash Flats. The presence of alternative foraging areas such as mud flats, barrier flats,

marsh edges, overwash pools, and other moist soil habitats close to nesting sites may benefit piping plovers during incubation by allowing both the foraging adult and the incubating adult to be available to participate in defense of the nest against predators (Cross 1988).

Early clutch initiation (21 April) in this study did not differ substantially from that reported by Patterson (1988) on Assateague Island in 1987 (18 April). MacIvor (1992) found that piping plovers in Massachusetts initiated clutches for 14 weeks including initial nests as early as 20 April and re-nests from 17 May - 25 July, longer by 3 weeks than clutch initiation lasted in this study. Early clutch initiation dates do not appear to vary directly according to increases in latitude. Early clutch dates are similar (third week of April) in North Carolina, Virginia, and New Jersey (Burger 1987, Wrenn 1990, this study). Clutch initiation was, however, a week earlier on Long Island (Wilcox 1959) and two weeks later in North Dakota (Gaines and Ryan 1988).

Clutch date may be related to environmental factors such as food supply and therefore vary according to prevailing environmental conditions rather than merely latitude. Laying dates in other species of birds have been advanced by 4 - 7 days by offering supplemental food before laying (Källander 1974, Yom-Tov 1974).

Clutch size in birds may also be related to feeding conditions because the degree of development of the ovaries is

dependent on the feeding regime (Cavé 1968). I found average clutch size of completed clutches at Chincoteague NWR (3.69 eggs/nest) to be similar to results from other studies in North Carolina (3.58, Wrenn 1990), North Dakota (3.5 Gaines and Ryan 1988) and Virginia (3.64, Patterson 1988; 3.79, Loegering 1992). This suggests that piping plovers at Chincoteague are obtaining adequate food for development of egg clutches. Average clutch size was larger on the Wild Beach (3.84) than on the Hook (3.61). This is contradictory to the hypothesis of limited foraging opportunities on the Wild Beach.

Incubation lasted for a mean of 26.9 days (n = 28 nests, SE = 0.60, range = 18 - 32) beginning with laying of the last egg. The incubation period was similar in length to that reported in other studies throughout the range (MacIvor 1990, 27.4 days; Haig and Oring 1988b, 25.7 days; Whyte 1985, 28 days). I frequently observed birds incubating one and two egg clutches but did not observe full-time incubation until 3 or 4 eggs were present. The average incubation period was shorter on the Hook (25.9 days, SE = 0.86) than it was on the Wild Beach (28.3 days, SE = 0.80). The difference, however, was not significant (Mann-Whitney U = 133.5, n_1 = 13, n_2 = 12, P = 0.0569). Cairns (1982) insinuates that protracted incubation periods in piping plovers may result from delays in incubation as in European Oystercatchers (Haematopus ostralegus) and spotted sandpipers (Actitus macularia)(Keighley and Buxton

1948, Hays 1972). Delays in incubation may occur frequently on the Wild Beach if birds there are forced to spend more time foraging away from the nesting territory or defending against predators.

There was no difference in hatching success between 4 egg and 3 egg clutches. Piping plovers appear to hatch synchronously and they make equal investment in all offspring. Brood reduction results when young are hatched asynchronously producing a size hierarchy and differential survival within broods (Lack 1954). Wilcox (1959) noted that piping plovers lay large final eggs. Piping plovers appear to have adapted a brood survivalist strategy where large eggs produce large, competitive offspring (Hill 1980, Clark and Wilson 1981).

Hatching success varied substantially among nesting areas during this study and was highest on the Wild Beach (Table 1.6). Overall hatching success (61.3%, n = 465 eggs) was lower than that reported in some studies (92% in Wilcox 1959, n = 668 eggs)(70% in Patterson 1988, n = 202 eggs)(72% in Cairns 1982, n = 104 eggs) but was much higher than that reported by MacIvor (1990) in Massachusetts (25%, n = 565 eggs) or Loegering (1992) in Maryland (35%, n = 284 eggs).

Hatching rates in this study were high in every year (range = 1.64 - 2.07 chicks hatched per nest, n = 141 nests, 3 yrs.)(Table 1.6). However, some nesting areas experienced low hatching success in some years (Hook, 1.09, 1990; Wash Flats, 0.91, 1991) due mostly to storm flooding and nest

abandonment. Haig and Oring (1988b) found a hatching rate of 1.1 chicks hatched per nest (n = 73 nests) in Manitoba at 10 sites from 1982 - 1985. Comparatively high hatching success and hatching rates at Chincoteague NWR probably reflect the general success of predator exclosures at protecting most nests until hatching. Many authors observed high clutch destruction by predators (Haig and Oring 1988b, Loegering 1992, MacIvor 1990).

Piping plovers are known to re-nest frequently after losing a clutch of eggs. Haig and Oring (1988b) observed piping plovers re-nesting up to 2 times after nest destruction in Manitoba but never observed more than one brood per season. MacIvor (1990) reported piping plovers nesting up to 6 times in one season in Massachusetts and between 60 and 82% of piping plovers in that study re-nested at least once.

Re-nesting at Chincoteague was most frequent in 1990 when 36% (n = 42 pairs) of all piping plovers re-nested at least once and least frequent in 1989 when only 13% of all pairs (n = 32) re-nested. Half of the piping plover pairs (50%, n = 14) that re-nested in the same territory after losing eggs in 1990 did so after the previous nest was destroyed by flooding. Haig (1987) and Strauss (1990) both reported that piping plovers were more likely to re-nest in the same territory if the prior nest was lost to predation rather than flooding.

Re-nesting may have been more common if piping plovers moved to other islands or states after nest failure and

therefore went undetected by this study. Haig (1987) found that 52% of all piping plovers in her study area re-nested but 41% of those adults which lost nests subsequently disappeared from the study site altogether. Patterson (1988) observed a small influx of piping plovers in Maryland in late June and July which he believed were coming from other nesting areas after failed nest attempts.

Patterson (1988) believed that piping plovers often re-nested on the Wash Flats after losing nests on the Wild Beach. I found only one case where plovers followed that scenario. Most known re-nests in this study (86%, n = 29) were found in the same nesting area as the original nest.

I observed no double-brooded (i.e. raising a second brood after a first brood fledges successfully) piping plovers, but I recorded 4 instances where piping plovers re-nested after hatching chicks at initial nests and losing them before fledging. MacIvor (1990) reported one observation of this behavior in piping plovers on Cape Cod. J. Kumer (pers. Comm.) reported two instances of re-nesting on Assateague Island, Maryland in 1994 which occurred after young fledged successfully from initial nests.

Piping plovers and Wilson's plovers (C. wilsonia) (Bergstrom 1988) exhibit biparental social systems and are generally single brooded. Some plovers are commonly double brooded. Mountain plovers (C. montanus) and snowy plovers (C. alexandrinus) are double brooded, but they exhibit single

parent incubation or brood care (Graul 1973, Warriner et al. 1986) freeing the other parent to mate again.

The frequency at which I observed renesting after brood loss is probably a result of the rate at which I protected egg clutches with predator exclosures (see Part 2). Eggs often hatched successfully from early nests protected with predator exclosures, allowing enough time for second clutches within the same nesting season. It is likely that double broods will be reported more frequently as the use of predator exclosures is encouraged throughout the plovers' range.

Few researchers have been able to document any direct causes of chick loss for piping plovers. Loegering (1992) reported one chick almost certainly depredated by a ghost crab on Assateague Island. Crushing by vehicles is commonly reported where vehicles and piping plovers use the same beaches (Goldin et al. 1988, Patterson 1988, Hoopes et al. 1990, Strauss 1990). Patterson (1988) was not able to identify any factors leading to chick mortality at Chincoteague NWR, Virginia except one chick found crushed by a vehicle.

I observed firsthand only two confirmed depredations of piping plover chicks, both by fish crows. I witnessed numerous chases and capture/release attacks of piping plover chicks by ghost crabs. However, 98.6% of all identifiable chick loss in this study was based on suggested causes rather than direct observations of the causal event.

I found fledging success to be highest in 1989 (1.13 chicks fledged per nesting pair) after escalating the use of predator exclosures to 100% of all nests on the Hook. Prior to that, fledging success was estimated at 0.19 on the Hook (Patterson 1991) and 0.84, n = 32 prs. (USFWS 1988b). Fledgling productivity appears to improve with the increased use of predator exclosures. However, productivity dropped sharply in 1990 (0.57) and recovered only slightly in 1991 (0.79) despite the continued use of predator exclosures. Losses to productivity were much higher after hatching than during incubation. Predator exclosures offer no protection to precocial chicks after they leave the nest.

Between nesting areas, fledging success was highest on the Wash Flats (44%) for the three years of this study and the highest fledging rate (1.66 chicks fledged per pair) was recorded there in 1989 (Table 7). Chicks on the Wash Flats may have realized a survival advantage from the wide, flat, and relatively un-vegetated brood-rearing areas of the Wash Flats which made it difficult for predators to approach broods without being detected. Further, chicks on the Wash Flats seemed to overcome any hardships to survival imposed upon them by the need to move long distances (range = 150.0 - 778.0 M) in the first week after hatching in order to find moist soil foraging habitats. In contrast, Strauss (1990) found that the probability of fledging nearly doubled for chicks which moved less than 200 M compared to those which moved more than 200 M

from the nest. However, hatching rates on the Wash Flats were lower than other nesting areas and the total number of chicks produced there was small.

Most mortality of piping plover chicks (68.2%, n = 176) occurred in the first 6 days after hatching. This finding is consistent with other studies. Loegering (1992) found 75% of chick mortality occurred in the first 6 days. MacIvor (1990) reports that 59% of chick mortality at her study sites on Cape Cod, Massachusetts occurred during the first 7 days after hatching. Wrenn (1990) reported 78% of chick mortality occurred in the first 8 days after hatching in North Carolina. I further discovered that much of my chick loss (27.7%, n = 176) was occurring on the first day after hatching and I therefore speculate that scents and behaviors associated with hatching may have attracted predators to some newly hatched chicks in the nest.

Some authors (Tull 1984, MacIvor 1990) have reported that chicks are more likely to fledge from nests initiated early in the season. I also found this to be true in 1989 and in 1991 when reproductive success was compared in six successive ten day periods (Table 1.9) but not in 1990. These results suggest that chicks hatched from early nests may realize increased survival probabilities by avoiding peak predator pressures in the early stages of development when they are most vulnerable to predators. Burger and Jenkins (1987) found piping plovers in New Jersey to be generally more successful if they nested

early in the season and attributed the difference to (1) advantages of nesting before the peak of human disturbances and (2) more time available to early nesters to gain weight before migration.

Piping plover reproductive success was constrained during this study by natural climactic conditions and tidal surges which resulted in occasional flooding of all nesting areas, predation, and to some extent availability of nesting habitat. The availability of nesting habitat may be of more critical importance if the functional availability is considered as well as the physical availability. Nesting habitat can be functionally unavailable due to predator pressure, foraging deficiencies, habitat alterations, disturbance or other factors which preclude nesting (S. Melvin, pers. comm.). In some regions, development may affect the availability of nesting habitat by forcing piping plovers to nest in sub-optimal habitats (MacIvor 1990).

Flooding of nests was a major cause of egg loss in 1990 (Table 1.12) when 81% (n = 43) of all flood losses occurred. Most flooding of eggs (63%, n = 35) in that year occurred on the Hook. Flooding accounted for 24% of all eggs lost during this study (n = 180). Overwashing of nests was a source of mortality in 6 years of an 8 year study of piping plovers in Massachusetts (Strauss 1990). But Loegering (1992) reported only 7% (n = 124) of piping plover egg loss in Maryland was due to flooding.

In 1990, I attempted to rescue two complete clutches of eggs on the Wash Flats after they were submerged in standing rainwater for > 12 hours. I removed the eggs and built mounds of sand to a height above the water level, then replaced the eggs. In both cases the adults resumed incubation of the flooded nests. One nest subsequently produced hatchlings but the other did not.

Many coastal, ground nesting birds are subject to nest loss from flooding (McNicholl 1985). Bildstein et al. (1991) suggest that piping plovers may face a decrease in numbers due to rising sea levels and habitat loss caused by global warming which may cause some barrier islands to migrate landward and others to break apart and disintegrate. However, Watts (1991) suggests that piping plovers are dependent on major disturbances (e.g. storms and tidal surges) to create the open, un-vegetated overwash fans that they often prefer as nest sites. Within nesting seasons, piping plovers may quickly recover catastrophic flood losses through the renesting process, whereas losses to predation or human disturbance tend to continue or increase throughout the nesting season. However, the long term loss of habitat for piping plovers due to natural geophysical processes has not been addressed.

The most serious proximate threat to piping plover nesting productivity in many areas may be predation (Patterson 1991). The effects of predation on egg loss in this study were confounded by the use of predator exclosure (see Part 2) which

prevented many predators from reaching the eggs but not from affecting nest success. Predators removed ≥ 1 egg from 35% (n = 141) of all nests despite the use of predator exclosures on 102 nests. Most often, egg loss due to predators (70%, 33/45 eggs) resulted from birds. Although it was difficult to identify individual avian predators, fish crows, boat-tailed grackles, and red-winged blackbirds were all implicated. These birds were all capable of penetrating predator exclosures.

Red foxes have been identified as the leading predator of piping plover nests in many studies (MacIvor 1990, Strauss 1990, Loegering 1992). Red foxes were not a serious direct threat to piping plover nests protected by predator exclosures in this study. They accounted for 27% (12/45) of all eggs lost to predators but only 7% (12/180) of total egg loss, mostly at un-exclosed nests. However, the greatest cause of egg loss was nest abandonment (29% (52/180) which may have been due to harassment of incubating adults by red foxes.

Patterson (1991a) identified raccoons as the major predator of piping plover nests on the Wild Beach (11 of 14 nests) in 1987. Although raccoons were frequently observed in our study areas, they accounted for negligible nest predation (2 eggs, 1% of total egg loss). Predator exclosures were effective at preventing raccoons from reaching nests and trapping may have been effective at limiting their numbers. Further, tracks indicated that raccoons most often crossed the dunes and proceeded directly to the water's edge to search for

food and thus missed many piping plover nests. Red foxes, on the other hand, travelled the length of the beach along the base of the dunes, often encountering piping plover nests and broods.

Red foxes were more effective than raccoons as predators of piping plover chicks in this study, accounting for an estimated 35% (69/197) of all chick loss. In addition red foxes were known to have killed at least two incubating adult piping plovers in 1991. Red foxes were active in all nesting areas. Considering their contributions to lost productivity during incubation and brood-rearing as well as their preying on adults, they probably represent the most serious and long-lasting limiting factor at Chincoteague NWR. Trapping may have been an effective control measure for raccoons in this study. I could attribute no chick loss to raccoons.

Piping plover populations at Chincoteague NWR will not realize the full advantage of improvements in hatching success stemming from the use of predator exclosures until the sources of chick loss can be more fully understood. Although I am confident that significant chick mortality is occurring due to predation, I acknowledge that some chicks may have been weakened by foraging deficiencies, rendering them more vulnerable to predators. Loegering (1992) believes that food availability plays a more important role in chick survival than predation on Assateague Island in Maryland. Even though sufficient food may be available to chicks in all nesting

areas at Chincoteague NWR, the risk of predation may sometimes prevent chicks from reaching the most profitable foraging sites. I suspect that predation and food availability are two interwoven factors which limit chick survival at Chincoteague NWR.

My estimates of fledgling productivity (0.57 - 1.13, n = 3 yrs.) remain below the level calculated by Gaines and Ryan (1988) (1.15 - 1.44) as the minimum necessary fledging rate to maintain population stability. Melvin and Gibbs (1994) developed a stochastic population model based on empirical survival rates and estimated a mean annual fecundity of 1.245 chicks fledged per pair as necessary to maintain a stable population. With moderate improvements in the protective efforts provided by predator controls piping plovers at Chincoteague NWR are expected to meet and exceed the levels of reproductive success necessary for population improvements.

PART 2. PREDATOR MANAGEMENT

Piping plovers (Charadrius melodus) on the Atlantic seaboard are beach nesting birds that experience heavy mortality from mammalian and avian predators during incubation (USFWS 1988, Patterson 1988, MacIvor 1990, Strauss 1990, Melvin et al. 1992, see Part 1). Many ground-nesting birds are especially vulnerable to predation of eggs or chicks (Lack 1968). Although the ultimate influence of predators on piping plover population dynamics is not known, losses to predation may result in decreased breeding success and local breeding population declines (Rimmer and Deblinger 1990). Recently, predator exclosures have been introduced as one way to undermine the declines in productivity due to egg predators. Early experiments have linked improved hatching success with exclosure use (USFWS 1988, Gelvin-Innvaer 1990, Melvin et al. 1992). Rimmer and Deblinger (1991) report that predator exclosures were, for the most part, effective at reducing predation in a survey of 211 exclosed piping plover nests (10% depredated) on the Atlantic coast in 1990. But the responses of piping plovers and their predators over time to the increased use of predator exclosures have not been investigated. In some cases, escalating or expanding predator

populations may be related to human activities (Erwin et al. 1981, Safina and Burger 1985).

Predator exclosures were used with limited success to protect nests of killdeer (Charadrius vociferous) in 1978 (Nol and Brooks 1981) and a modified design was first applied to 7 piping plover nests at 4 Atlantic coast sites in 1987. With initial trials proven successful, the use of predator exclosures increased to over 70 at 14 sites on the Atlantic coast in 1988 (Atlantic Coast Piping Plover Recovery Team 1994).

In this study, I employed predator exclosures to protect piping plover nests at Chincoteague National Wildlife Refuge (Chincoteague NWR), Assateague Island, Virginia from 1989 to 1991. Prior to this study, in 1986 and 1987, 54% of all piping plover nests on Assateague Island were unsuccessful and 91% of all known nest losses were attributed to predators (Patterson et al. 1991a). First use of predator exclosures at Chincoteague NWR occurred in 1988 on 20 (57%) piping plover nests (USFWS 1988) resulting in 85% nest success (≥ 1 egg hatched). Subsequently, exclosures were slated for use on more piping plover nests at Chincoteague NWR in the next three years.

In order to further increase the likelihood of improving nesting success for piping plovers I continued and escalated a trapping program for red foxes and raccoons which had been initiated in 1986. Indices of red fox abundance measured in

1988 suggested that red foxes were increasing at Chincoteague NWR despite increased harvests of red foxes in that year (USFWS 1988). I targeted individual animals responsible for piping plover nest and chick predation by trapping only along the perimeters and within identified nesting areas. Unfocused trapping efforts are not likely to be successful in influencing nesting productivity for piping plovers (Patterson 1990).

Red foxes and raccoons are the only mammalian predators known to prey upon piping plovers at Chincoteague NWR (Patterson 1988, USFWS 1988). However, numerous avian predators and one crustacean predator, the ghost crab (Oncypoda quadrata) are potentially harmful. Of these, the ghost crab may be the most significant at Chincoteague NWR. Ghost crabs were implicated as the main predator of piping plover chicks on the Wild Beach in 1988 when 31 of 32 (97%) chicks were lost to unknown causes (USFWS 1988). I surveyed the ghost crab population on the Wild Beach in all three years of this study to determine abundance and population trends. I also observed interactions between ghost crabs and piping plovers during daylight hours to detect any attempted predation of piping plovers by ghost crabs.

This section (1) reports on the long term efficacy of non-lethal and lethal predator controls for the protection of piping plover nests (2) discusses some behavioral responses of piping plovers and their predators to predator exclosures, and

(3) suggests some guidelines for the continued use of predator exclosures and trapping as management practices.

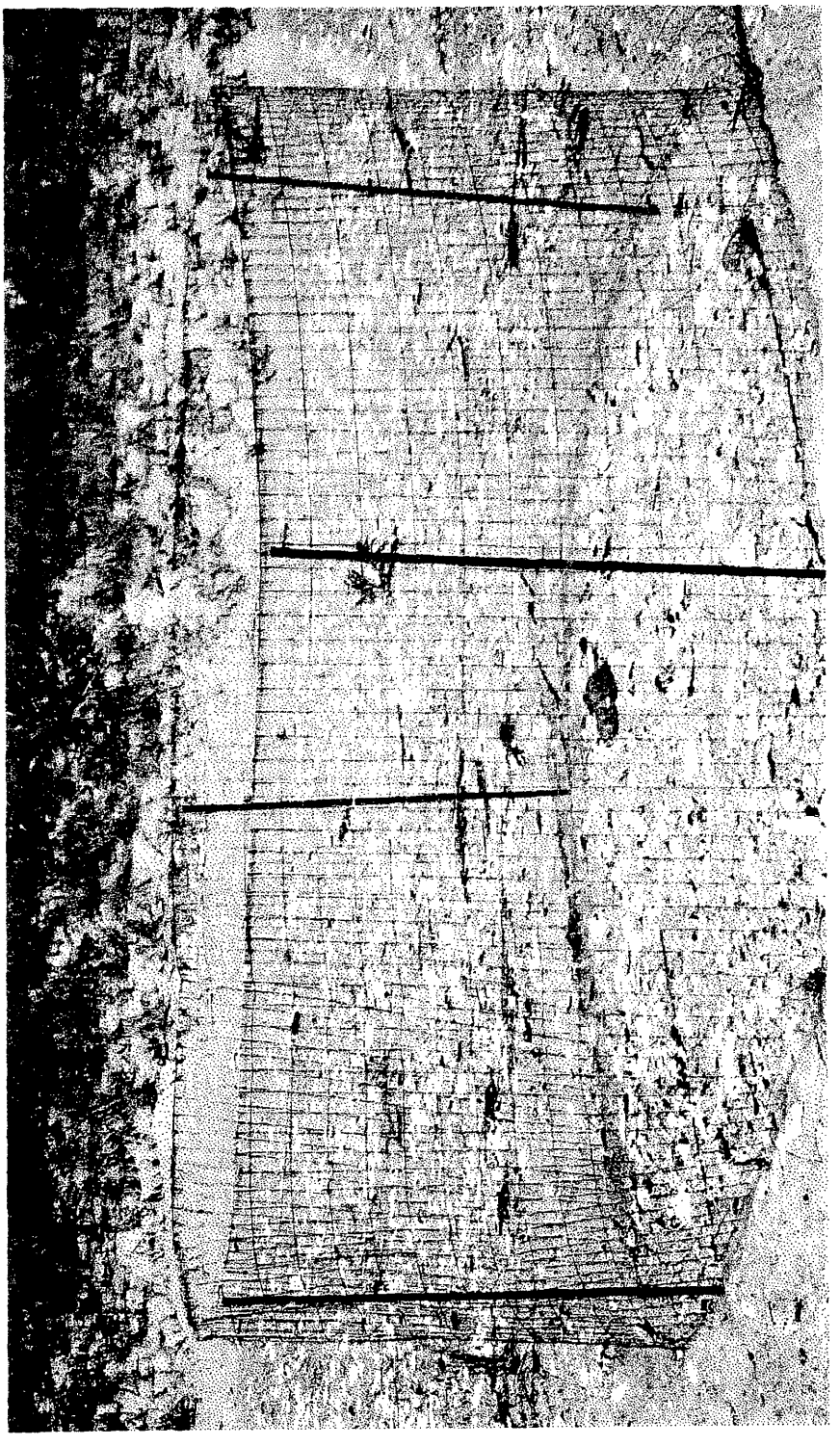
METHODS

PREDATOR EXCLOSURES

Protocols for the use of predator exclosures were determined prior to each nesting season and were based on assessment of predator losses in the previous year. In 1989, predator exclosures were slated for use on 100% of nests found on the Hook and 50% of nests found on the Wild Beach and Wash Flats. In 1990 and 1991, predator exclosures were prescribed for use on 100% of all nests in all nesting areas in an attempt to maximize productivity. The actual proportion of nests treated with predator exclosures was less than prescribed since some nests were destroyed before predator exclosures could be erected.

Predator exclosures were constructed of 122 cm tall, 5 cm x 10 cm welded wire fencing precut to 9.8 m length to form a 3.1 m diameter circular exclosure (Figure 2.1). I placed a 30 cm diameter, ventilated plastic bowl over the nest and stabilized it with 2 sand spikes to shade the eggs and protect them from accidental damage during exclosure construction. The exclosures were buried 10 cm deep in the ground and were supported by 4, 1.5 m long steel "rebar" driven approximately

Figure 2.1. Piping plover predator exclosure.



41 cm in the ground with a sledge hammer. Sixty pound test monofilament fishing line was woven across the exclosure top at 10 cm - 15 cm intervals to deter avian predators. Two, three, or four persons participated in exclosure construction. All ground level openings were inspected before leaving to ensure open access to adult piping plovers and tracks were swept away from the area to prevent attraction of predators to the nest. Predator exclosures were not constructed during inclement weather or periods of extreme temperatures.

The time required for exclosure construction was recorded in all three years as was the time elapsed until one adult returned and resumed incubation. All exclosed nests were observed with telescope or binoculars after construction of the exclosure until incubation was resumed. If an adult piping plover did not return to the nest within 60 min. of completion of exclosure construction, the exclosure was removed and was not replaced.

Nests were monitored daily. When hatching dates could be predicted, nest monitoring was less frequent in weeks 2 and 3 of incubation than in weeks 1 and 4. Broods were monitored daily or nearly daily from hatching until ≥ 25 days old to determine annual productivity as chicks fledged per nesting pair. Nests were considered successful if at least one egg hatched and unsuccessful if no eggs hatched. Differences in nest success at exclosure-treated nests were evaluated using

G tests (Sokal and Rolfe 1981) based on an equal probability of the nest hatching or not hatching.

In 1989, exclosures were erected only after 4 eggs or complete clutches were observed. But in 1990 and 1991, after observing high egg loss prior to clutch completion, nests were protected with exclosures after the third egg was deposited Smaller clutches were protected if no further egg laying occurred after three consecutive days.

Red foxes and raccoons were trapped from perimeters and within the three piping plover nesting areas. Trapping was conducted beginning on 3 March, 1989, 1 February 1990, and 18 January 1991 and continued through July of each year. I used steel jawed, double jawed, and "soft catch" leg hold traps (size 1½ and 2) anchored with 45 cm angle-iron stakes at bait holes to capture red foxes. Traps were placed according to fox travel patterns, baited with fish parts, and enhanced with a commercially produced fox lure product. Raccoons were trapped with the same leg hold traps and with "Have-a-heart" live capture traps.

All traps were checked daily in the early AM. Captured red foxes and raccoons were killed and buried on site to prevent the attraction of other predators or scavengers into nesting areas. Traps were closed during inclement weather or if they could not be checked daily. Non-target animals caught in traps were released. Raccoons and red foxes were also shot when encountered in the field.

The causes for any egg loss or abandonment were determined by searching the site for evidence of disturbance, flooding, or predation including predator tracks, egg content remains or eggshell fragments, or other evidence suggesting that a predator had breached the exclosure or killed an adult piping plover. Although observations of actual predation events were rare, observations of predators active in each nesting area were helpful in improving confidence that identification of nest predators was accurate.

Ghost crab surveys were conducted on the Wild Beach during July or August of each year after most piping plover chicks had fledged or disappeared in order to avoid disturbance to nesting pairs of piping plovers or their young. I surveyed for ghost crabs only within the segment of beach occupied by piping plovers. Surveys were performed by counting all active ghost crab burrows within 0.04 ha circular plots at 0.24 km or 0.48 km intervals along the length of the beach. This indirect method of approximating the population was chosen over nocturnal observations due to the difficulty in observing rapid movements of surface-active crabs (Wolcott and Wolcott 1984). Burrow counts also estimate the entire population rather than only those crabs active on the surface. Burrows were determined as active if fresh tracks were present on freshly mounded sand at the burrow entrance (Wolcott 1978). The plot centers were chosen by visually selecting the

greatest burrow density along a linear transect perpendicular to the wrack line.

RESULTS

PREDATOR CONTROL (NON-LETHAL)

Predator exclosures were constructed at 102 piping plover nests (380 eggs) in this study (Table 2.1). The earliest date of exclosure construction was 28 April and the latest date was 10 July. Exclosure use increased each year (26, 1989; 37, 1990; 39, 1991) owing partially to procedural changes allowing earlier protection of incomplete egg clutches and partially to changes in the protocol for exclosure use. Most nests (92%, n = 26) exclosed in 1989 contained 4 egg clutches, but in 1990 and 1991, 37 exclosures (49%, n = 76) were placed on nests with fewer than 4 eggs. The mean clutch size for all exclosure treated nests was 3.6 eggs (SE = 0.06, range = 1 - 4, n = 102). There was no significant difference in the hatching success of the nest if it was exclosed with 1, 2, 3, or 4 eggs (Kruskal Wallis test, Chi-square approximation, $X^2 = 2.2905$, $P = 0.5143$, $df = 3$).

Construction of predator exclosures required a mean of 15.0 min. (SE = 20 sec., range = 8 min. 30 sec. - 23.0 min., n = 90). Adult piping plovers resumed incubation quickly (mean = 8 min. 13 sec., SE = 71 sec., range = 44 sec. - 60 min., n

= 86) after exclosure construction. But, in two instances (2%), adult plovers did not resume incubation within 60 min. of completion of exclosure construction. In each case, the adults returned to incubate when the exclosure was removed but both nests were subsequently depredated within three days. One of these cases involved an incubating male that was missing the right foot and tarsus.

Exclosures were used most frequently (57%) on the Hook followed by the Wild Beach (24%), and the Wash Flats (19%). Forty-nine treated nests (48%) experienced some egg loss. The percentage of exclosure treated eggs lost in each nesting area varied from 0% on the Wild Beach in 1989 to 71.1% on the Wash Flats in 1991. In total, 137 exclosed eggs (36.1%) were lost to various causes and did not hatch (Table 2.1).

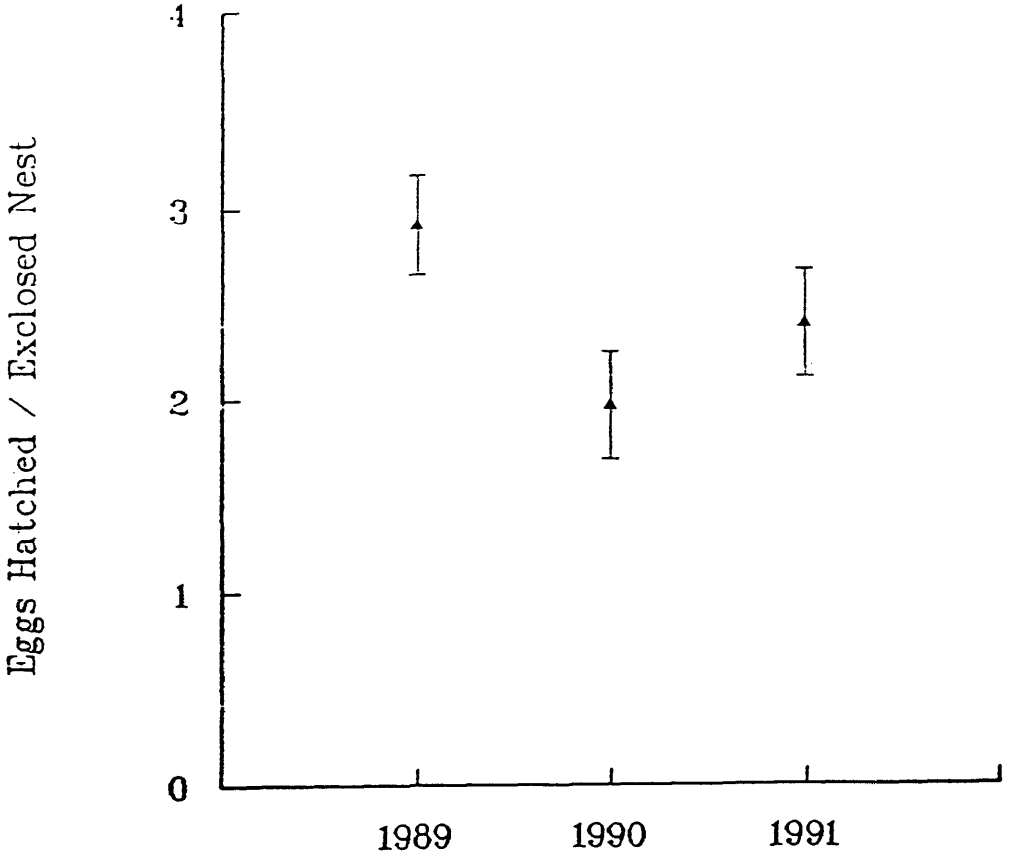
Hatching rates at exclosed nests varied between years in each nesting area (Figures 2.2, 2.3, 2.4) ranging from 1.10 eggs hatched / nest on the Wash Flats (1991) to 4.0 eggs hatched / nest on the Wild Beach (1989). In comparisons of exclosed nests between nesting areas (Table 2.2), hatching rates were usually highest on the Wild Beach (range = 3.125 - 4.0 eggs hatched / nest) but were highest on the Wash Flats in 1989. The difference in hatching rates between nesting areas was significant in 1991 (ANOVA, $P = 0.020$). There were, however, no significant differences detected in the number of eggs produced / nest or in the number of chicks fledged / nest

Table 2.1. Egg production and egg loss to all causes at exclosed piping plover nests at Chincoteague NWR, 1989 - 1991.

Area	Year	No. Nests	No. Exclosed Nests	%	No. Eggs	No. Exclosed Eggs	%	No. Exclosed Nests Losing ≥ 1 Egg	%	No. Exclosed Eggs Lost	%
Hook	1989	20	19	95.0	75	73	97.3	12	63.2	23	31.5
	1990	33	18	54.6	91	63	69.2	12	66.7	35	55.6
	1991	25	21	84.0	83	76	91.6	5	23.8	18	23.7
Wild	1989	8	3	37.5	25	12	48.0	0	0.0	0	0.0
Beach	1990	16	13	81.3	54	48	88.9	3	23.1	12	25.0
	1991	9	8	88.9	33	32	97.0	2	25.0	7	21.9
Wash	1989	8	4	50.0	27	16	59.3	2	50.0	2	12.5
Flats	1990	10	6	60.0	34	22	64.7	6	100.0	13	59.1
	1991	12	10	83.3	43	38	88.4	7	70.0	27	71.1
Refuge	1989	36	26	72.2	127	101	79.5	14	53.9	25	24.8
	1990	59	37	62.7	179	133	74.3	21	56.8	60	45.1
	1991	46	39	84.8	159	146	91.8	14	35.9	52	35.6
Totals		141	102	72.3	465	380	81.7	49	48.0	137	36.1

Figure 2.2. Number of eggs hatched per nest (mean and standard error) at exclosed piping plover nests on the Hook, 1989 - 1991 (n = 19, 18, 21).

Figure 2.3. Number of eggs hatched per nest (mean and standard error) at exclosed piping plover nests on the Wild Beach, 1989 - 1991 (N = 3, 13, 8).


Eggs Hatched / Exclosed Nest
4
3
2
1
0
1989
1990
1991

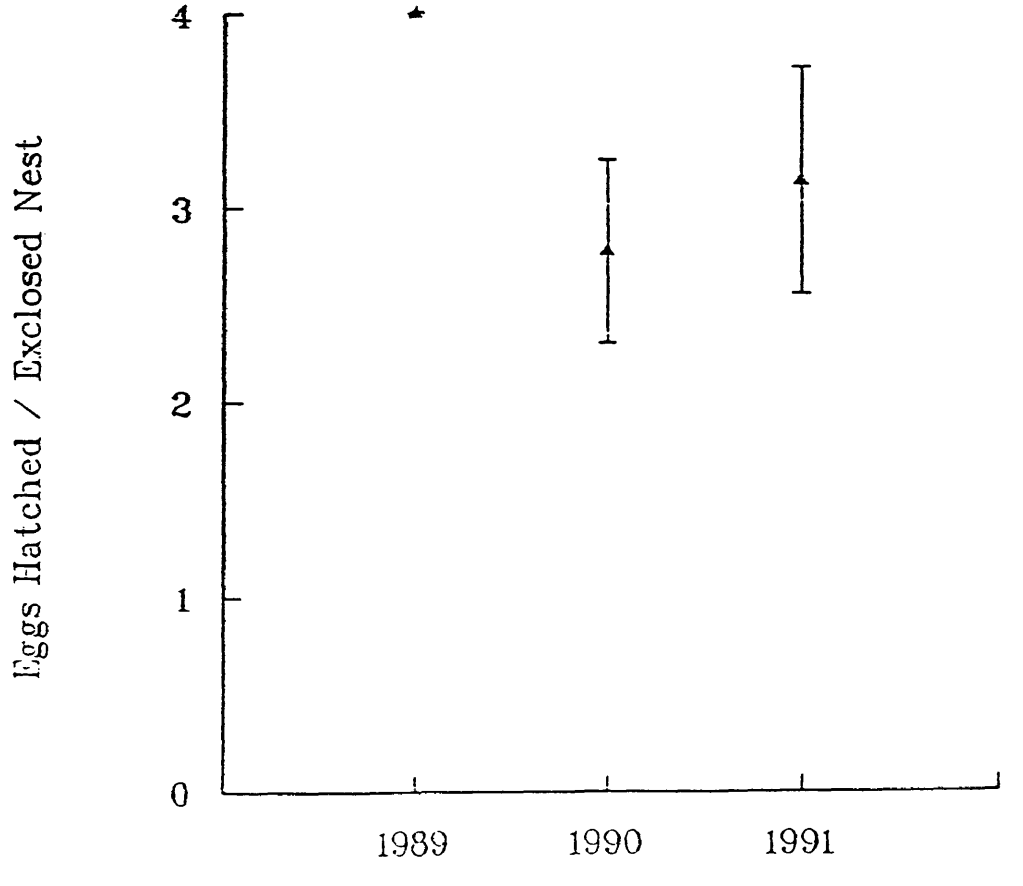
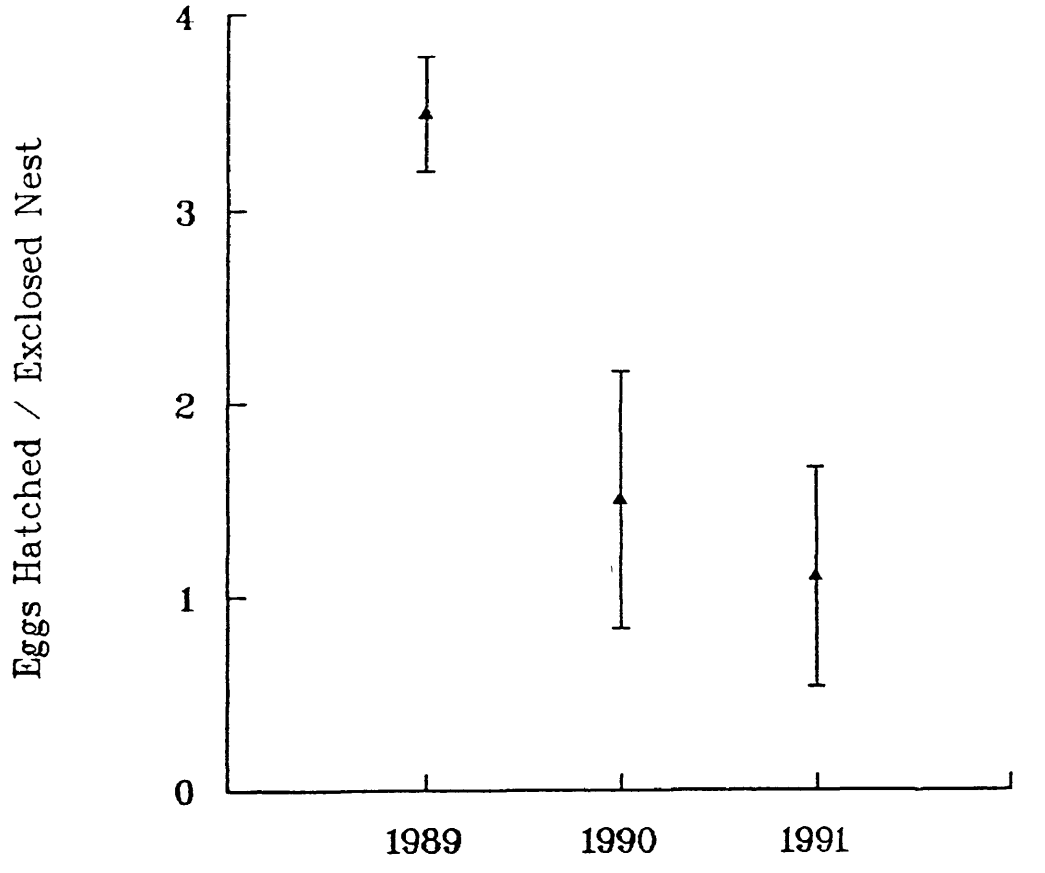

Eggs Hatched / Exclosed Nest
4
3
2
1
0
1989
1990
1991

Figure 2.4. Number of eggs hatched per nest (mean and standard error) at exclosed piping plover nests on the Wash Flats, 1989 - 1991 (n = 4, 6, 10).

Figure 2.5. Number of eggs hatched per nest (mean and standard error) at exclosed piping plover nests at Chincoteague NWR, 1989 - 1991 (n = 26, 37, 39).


Eggs Hatched / Exclosed Nest
4
3
2
1
0
1989
1990
1991

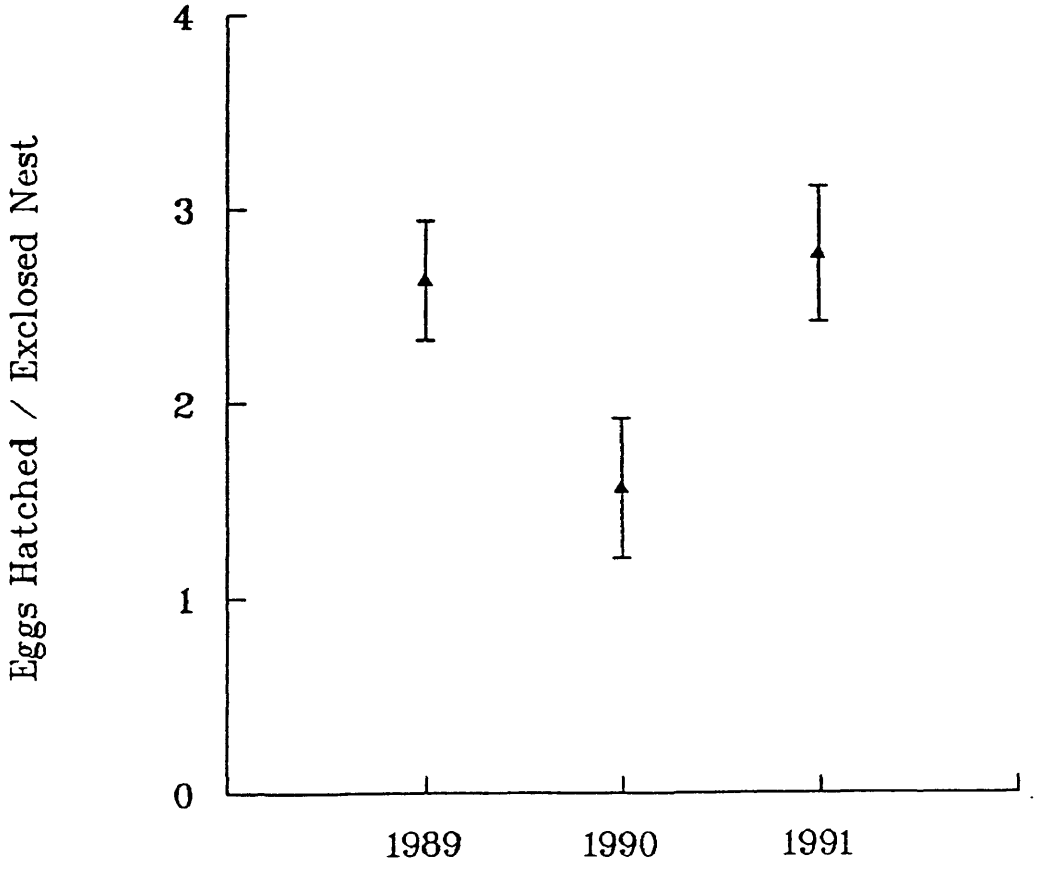

Eggs Hatched / Exclosed Nest
4
3
2
1
0
1989
1990
1991

Table 2.2. Comparisons of egg production, hatching success, and fledging success between nesting areas at exclosed piping plover nests at Chincoteague NWR, 1989 - 1991.

	1989						1990						1991					
	Eggs/Nest		Hatched/Nest		Fledged/Nest		Eggs/Nest		Hatched/Nest		Fledged/Nest		Eggs/Nest		Hatched/Nest		Fledged/Nest	
Area	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Hook	3.8	0.08	2.6 A	0.30	1.1	0.30	3.5 A	0.16	1.5 A	0.36	0.7 A	0.24	3.6	0.12	2.7 AB	0.34	0.9 A	0.27
Wild Beach	3.5	0.5	3.0 A	1.0	0.0	0.0	3.6 A	0.17	2.7 A	0.46	0.1 A	0.10	4.0	0.0	3.1 A	0.58	0.3 A	0.18
Wash flats	4.0	0.0	3.5 A	0.28	1.0	0.70	3.6 A	0.21	1.5 A	0.67	0.5 A	0.34	3.8	0.13	1.1 B	0.56	0.8 A	0.41
F			0.701				0.368		2.450		1.819				4.40		0.598	
P			0.506				0.695		0.101		0.178				0.020*		0.555	
df			26				36		36		36				38		38	

[1] One-Way Analysis of Variance
Means with same letters are not significantly different (P > 0.05, Tukey HSD Multiple Comparison).
ANOVA could not be performed where one or more groups lack variance.

Sample Sizes (Exclosed Nests)

	Hook	Wild Beach	Wash Flats	Year Totals
1989	19	3	4	26
1990	18	13	6	37
1991	21	8	10	39
Area Totals	58	24	20	102

at exclosed nests between different nesting areas in any year. A significant positive correlation (Pearson's product/moment correlation, r = 0.441, P = 0.0021) was found between the number of eggs hatched and the number of exclosures used. Considering all exclosed nests in all nesting areas (Figure 2.5) hatching rates were highest in 1989 and lowest in 1990 (range = 1.97 - 2.92 eggs hatched per nest), indicating a slight downward trend in the three years of this study.

Predator exclosures used to protect piping plover nests were most successful on the Wild Beach over the 3 years of this study (79.8% successful nests), followed by the Hook (73.5% successful nests). Nesting success at exclosed nests on the Wash Flats averaged somewhat lower (60.0% successful nests) largely due to poor results in 1991 (30.0% successful nests). In 1989, 88.4% of all exclosure-treated nests at Chincoteague NWR hatched successfully (Table 2.3). But treated nests were successful much less often in 1990 (62.2%) and in 1991 (69.2%). When treated nests from all three years are pooled, however, there were more successful nests (73.3%) than failed nests.

Egg predators identified included red fox, raccoon, fish crow, boat-tailed grackle, and red-winged blackbird. Egg loss at exclosed nests (Table 2.4) was attributed to abandonment (34.3%), flooding (19.7%), avian predation (16.8%, mostly crow), infertility (10.2%), wind drifted sand (9.5%), unknown causes (3.6%) and mammalian predation (2.9%, red fox). The

Table 2.3. Distribution and success of predator exclosures used to protect piping plover nests at Chincoteague NWR, 1989-1991.

Area	Year	Nests (N)	Exclosed Nests		
			No.	Successful Nests[1] (%)	Failed Nests[2]
Hook	1989	20	19	16 (84.2)	3
	1990	33	18	10 (55.5)	8
	1991	25	21	17 (80.9)	4
	Mean	26	19	14 (73.5)	5
Wild Beach	1989	8	3	3 (100.0)	0
	1990	16	13	10 (76.9)	3
	1991	9	8	7 (87.5)	1
	Mean	11	8	7 (79.8)	2
Wash Flats	1989	8	4	4 (100.0)	0
	1990	10	6	3 (50.0)	3
	1991	12	10	3 (30.0)	7
	Mean	10	6.67	3.33 (60.0)	3.3
Total Refuge	1989	36	26	23 (88.4)	3
	1990	59	37	23 (62.2)	14
	1991	46	39	27 (69.2)	12
	Mean	47	34	24 (73.3)	10

[1] Successful nests are those where at least one egg hatched.
[2] Failed nests are those where no eggs hatched.

Table 2.4. Causes of egg loss at exclosed piping plover nests at Chincoteague NWR, 1989 - 1991.

Area	Year	No. Of Exclosed Eggs Lost	No. Eggs Lost To:											
			Avian Pred.	%	Red Fox	%	Flood [1]	%	Wind	%	Infert.	%	Aband.	%	Unknown	%
Hook	1989	23	8	34.8	0	0.0	0	0.0	5	21.7	6	26.1	0	0.0	4	17.4
	1990	35	12	34.3	0	0.0	16	44.7	4	11.4	3	8.6	0	0.0	0	0.0
	1991	18	3	16.7	0	0.0	0	0.0	0	0.0	1	5.6	14	77.8	0	0.0
Wild	1989	0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Beach	1990	12	0	0.0	4	33.3	4	33.3	4	33.3	0	0.0	0	0.0	0	0.0
	1991	7	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	7	100.0	0	0.0
Wash	1989	2	0	0.0	0	0.0	0	0.0	0	0.0	2	100.0	0	0.0	0	0.0
Flats	1990	13	0	0.0	0	0.0	7	53.9	0	0.0	2	15.4	3	23.0	1	7.7
	1991	27	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	27	100.0	0	0.0
Refuge	1989	25	8	32.0	0	0.0	0	0.0	5	20.0	8	32.0	0	0.0	4	16.0
	1990	60	12	20.0	4	6.7	27	45.0	8	13.3	5	8.3	3	5.0	1	1.7
	1991	52	3	5.8	0	0.0	0	0.0	0	0.0	1	1.9	44	84.6	0	0.0
Totals		137	23	16.8	4	2.9	27	19.7	13	9.5	14	10.2	47	34.3	5	3.6

[1] Includes eggs flooded by tidal overwash and by rain water.

greatest causes of egg loss were abandonment of nests followed by flooding.

Red foxes caused the abandonment of 13 nests (Hook = 4, Wild Beach = 2, Wash Flats = 7) in 1991 accounting for 84.6% of all egg loss at exclosed nests in that year. At two of these nests the remains of adult piping plovers were found outside the exclosures amidst numerous red fox tracks. I believe red foxes killed these adults and may have killed adult piping plovers at other abandoned nests. Tracks observed at exclosures indicated that these were often young foxes probably from nearby dens.

I do not believe that nest abandonments were related to the process of exclosure construction. Most abandonments occurred long after exclosure construction was completed (mean = 16.6 days, SE = 6.28, range = 4 - 30 days, N = 13). Three nests (23.1%) were in the process of hatching when abandoned suggesting that foxes may have been attracted to increased activity at the nest near hatching time. More eggs were abandoned in 1991 (61%) on the Wash Flats, but there was no significant difference in the number of eggs abandoned between areas (Kruskal Wallis test, $X^2 = 0.9643$, P = 0.6175, df = 2).

Fox tracks were observed at 54% of exclosed nests during this study. Foxes frequently attempted to dig beneath predator exclosures while pacing at the perimeter. However, there was only one penetration of a predator exclosure by a red fox, resulting in the loss of 4 eggs. Foxes did not gain access to

any exclosed nests by climbing the exclosure. The number of exclosures visited by red foxes increased each year (1989, 37.0%; 1990, 48.7%; 1991, 72.5%) and more nests were abandoned due to foxes each year (0, 1989; 1, 1990; 13, 1991).

I found an increase in the number of eggs lost to predators each year, if eggs lost to abandonment are combined with eggs lost to predators (Figure 2.6). Total egg loss was variable between years but the difference in the number of eggs lost to predation and abandonment combined increased significantly ($G = 36.57$, $P < 0.001$, $df = 2$).

PREDATOR CONTROL (LETHAL)

Lethal removal of red foxes (mean = 25.3 ± 4.9 / year, range = 22 - 31) decreased predator pressure but not below any population threshold which would prevent predation of piping plover eggs and young.

I began removing red foxes earlier each year in an attempt to curtail breeding and subsequent population increase prior to piping plover breeding season (Table 2.5). In 1990 and 1991, most captures (70%, 77% respectively) occurred before piping plovers began laying eggs. Trapping was the most successful method of removing red foxes. Red foxes were removed in an equal sex ratio (33 males, 33 females) over the 3 year period suggesting that most foxes trapped were residents rather than foreign males seeking new territories.

Increases in the amount of effort expended in trapping did not result in increased trapping success for red foxes (Table 2.5). There was no significant difference between years in the number of red foxes removed ($G = 1.614$, $P > 0.05$, $df = 2$) despite more effort expended each year. I trapped for more days (143) and used more traps per night (21.46) in 1991 than in either of the previous years. However, the number of red foxes trapped per unit effort (trap night) decreased (0.010) in that year.

Raccoons were removed by trapping or shooting in greater numbers each year (mean = 89.0 ± 43.4 / year, range = 53 - 137)(Table 2.6). Trapping was the most successful removal method (74%), however, more raccoons were shot in each year. There was no evidence of raccoon predation at any exclosed piping plover nests in any year of this study. Raccoon tracks observed at exclosed nests indicated that raccoons often passed near exclosures but did not attempt to dig under or climb over the exclosure.

Trapping and shooting efficiency for raccoons was greatest in 1990 (0.049 raccoons per trap night) despite greater trapping effort expended in 1991. I removed more raccoons each year and the difference between years was significant ($G = 41.266$, $P < 0.001$, $df = 2$). Raccoons were not removed in equal sex ratios ($G = 16.312$, $P < 0.001$, $df = 1$). Of 267 raccoons removed by trapping or shooting, 166 (62%) were males and 101

Figure 2.6. Total number of eggs produced, lost to all causes, and lost to predation or nest abandonment at exclosed piping plover nests at Chincoteague NWR, 1989 - 1991.

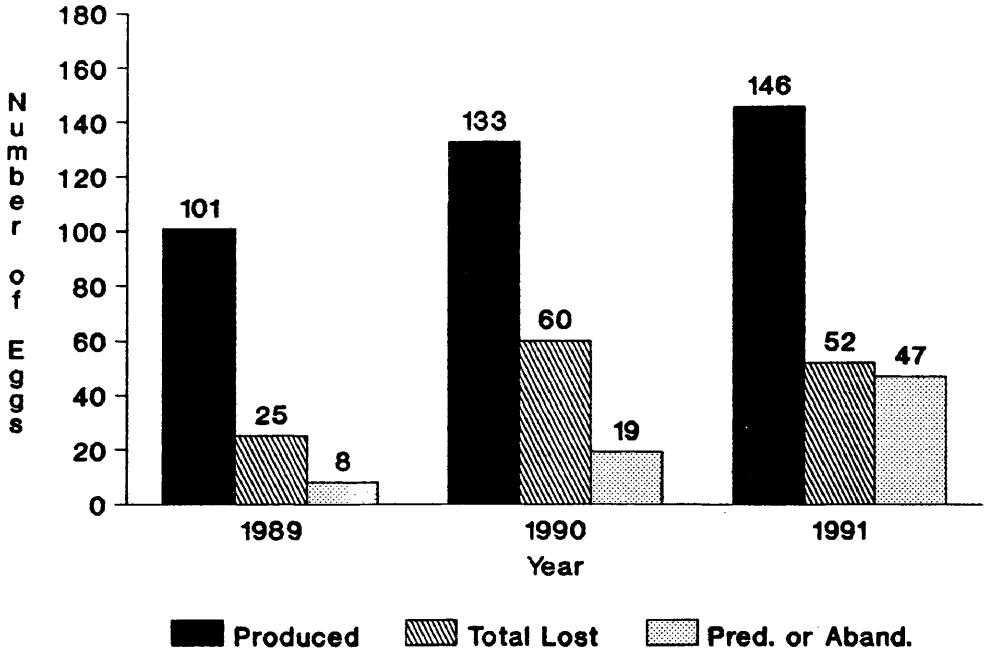

180
160
140
120
100
80
60
40
20
0
Number of Eggs
101
25
8
133
60
19
146
52
47
1989
1990
1991
Year
Produced
Total Lost
Pred. or Aband.

Table 2.5. Chronology and results of red fox removal at Chincoteague National Wildlife Refuge, 1989 - 1991.

	Date		
	3 Mar-16 July 1989	1 Feb-31 July 1990	18 Jan-23 July 1991
No. trapped	21	21	30
No. shot	1	2	1
Total taken	22	23	31
% taken before 21 April[a]	32	70	77
No. days	87	85	143
Mean traps/night[b]	16.89	18.13	21.46
range	6-31	5-40	1-55
SE	0.85	0.94	1.13
Trap nights[c]	1469	1541	3068
Foxes per trap night	0.015	0.015	0.010

[a] Date represents earliest piping plover clutch initiation.
[b] Includes leg hold traps and live traps.
[c] Trap night = 1 trap set for 1 night.

Table 2.6. Chronology and results of raccoon removal at Chincoteague National Wildlife Refuge, 1989 - 1991.

	Date		
	3 Mar-16 July 1989	1 Feb-31 July 1990	19 Jan-25 June 1991
No. trapped	50	53	94
No. shot	3	24	43
Total taken	53	77	137
% taken before 21 April[a]	87	92	88
No. days	87	85	143
Mean traps/night[b]	16.89	18.13	21.46
range	6-31	5-40	1-55
SE	0.85	0.94	1.13
Trap nights[c]	1469	1541	3068
Raccoons per trap night	0.036	0.049	0.045

[a] Date represents earliest piping plover clutch initiation.
[b] Includes leg hold traps and live traps.
[c] Trap night = 1 trap set for 1 night.

(38%) were females. Leghold traps were efficient at trapping raccoons (118/197, 60%), although, live traps were also effective (79/197, 40%).

GHOST CRAB SURVEYS

I surveyed ghost crab burrows on the Wild Beach once in 1989, 3 times in 1990, and 2 times in 1991, all in the months of July and August (Table 2.7). The mean number of burrows per 0.04 ha survey plot increased each year (range = 156.6 - 245.2 burrows per plot). The difference in the number of burrows per plot were significant in all yearly comparisons (Table 2.8). Ghost crab burrow counts also increased within years in 1990 and 1991 when multiple surveys were conducted.

Although ghost crab burrow counts showed some tendency to increase from south to north on the Wild Beach, piping plovers did not appear to select nest sites where ghost crab density was lowest. In 1989, I divided survey plots into two categories, those with a piping plover nest site within 100 m (n = 5) and those without a piping plover nest within 100 m (n = 19). There was no significant difference in the number of ghost crab burrows per plot between the two categories ($F = 3.37$, $P > 0.20$, $df = 24$). Further, in 1991 ghost crab burrow density was greatest at a mean distance of 12.15 m (SE = 0.88, n = 28) from the wrack line, whereas piping plover nests were found at a mean distance of 58.06 m (SE = 9.17, n = 8) from

Table 2.7. Results of ghost crab burrow surveys on the Wild Beach at Chincoteague NWR, 1989 - 1991.

Year	No. Of Surveys	Plots/ Survey	Total Plots	Plot Size (ha)	Ghost Crab Burrows Mean	SE	Range
1989	1	24	24	0.04	156.60	16.10	24-288
1990	3	8	24	0.04	208.20	16.50	81-354
1991	2	14	28	0.04	245.21	12.04	110-360

Table 2.8. Comparisons of ghost crab survey results 1989 - 1991.

Comparison	t	Probability
1989 vs 1990	3.20	< 0.01
1989 vs 1991	5.49	< 0.001
1990 vs 1991	2.24	< 0.05

the wrack line. Ghost crabs and piping plovers appear to use different areas of the beach during the incubation period for piping plovers. Further, piping plovers initiate courtship and territorial establishment before ghost crabs become active in the Spring.

Piping plovers were often observed defending chicks against ghost crabs by charging the crab with raised wings, by interfering with the crab's approach to vulnerable chicks, and by feigning injury to lure crabs away from chicks. During 8 hours of observing a brood of three chicks in July, 1989, I witnessed more than 80 agonistic interactions between ghost crabs and piping plover chicks or defending adults. It was unclear how many ghost crabs were involved in the interactions. Near captures of chicks by ghost crabs were frequent. The female adult piping plover suffered a leg injury causing her to limp for several days as a result of one interaction with a ghost crab. None of the three chicks survived to fledging age and were believed to have been captured by crabs.

DISCUSSION

Predator exclosures were accepted by piping plovers in this study and nests treated with exclosures were successful more often than not. Despite the increased use of predator

exclosures, predators caused greater egg loss at exclosure treated nests each year (32%, 1991; 20%, 1989-91).

At Chincoteague NWR, red foxes in particular showed increasing interest in exclosed piping plover nests. Red foxes on northern Assateague Island, Maryland depredated 44.0% of exclosure protected piping plover nests in 1990 and may have cued in on nests by locating the exclosures (Rimmer and Deblinger 1991, J. Loegering, pers. comm.). Distraction displays used by adult piping plovers and other lesser plovers (e.g. killdeer, Brunton 1986; Wilson's plover, Bergstrom 1988) are employed at some risk to the performing adult. Increased intensity of the distraction display with nesting stage and decreased distance of the display from the predator due to predator exclosures probably increase the risk to the defending adult. Rimmer and Deblinger (1990) used large, triangular exclosures (30 m perimeter) in Massachusetts, increasing the distance of predators from the nest and improving hatching success to 92%.

Further, disturbance at exclosed nests caused by marauding foxes may induce parental neglect, resulting in extended periods when young chicks or eggs are exposed to cold temperatures. Emlen et al. (1966) observed a single raccoon which was indirectly responsible for extensive egg and chick mortality in one night by causing "panic flights" in a colony of ring-billed gulls (Larus delawarensis). They estimated 30 to 80% nightly mortality of 1 - 2 day old chicks resulting

from exposure to 5° - 15° C temperatures during raccoon visits. Piping plover chicks which typically disappear at an early age may be weakened by exposure in predator-rich environments and fall victim eventually to predators or scavengers.

Predators are able to locate nests through parental activity (Skutch 1949), the sounds emitted by the young (Perrins 1965) or by scents from eggs, young, or adults at the nest (Lill 1974). Predators also locate nests of ground nesting birds visually (Lill 1974). MacIvor et al. (1990) observed that red foxes seemed to locate piping plover nests through chance encounters and systematic searches and not by following researcher tracks or scents. Mammalian predators may have found exclosed killdeer nests through attraction to the exclosure itself (Nol and Brooks 1982).

With the increased use of exclosures red foxes may encounter them more often, locate nests more easily, and/or learn to associate exclosures with food. If predator exclosures prolong the duration of fox visits by keeping them at bay, they may promote abandonment by adult plovers or increase their risk of being captured and eaten. Our abandonment rate (14%, n = 102 nests) was higher than expected based on other studies (11%, Cairns 1977; 10%, Vasque et al. 1992). However, abandonment was not a chronic problem at exclosed nests. Most (93%) nest abandonments occurred in a single year (1991).

I observed no ill effects from the use of monofilament line on top of exclosures. I observed two instances where an incubating adult flushed through the top but these birds were only impeded momentarily and were not injured. In all other observations piping plovers walked through the exclosures when entering or leaving. Vasque et al (1992) found a significantly higher probability of nest abandonment at exclosed nests where monofilament tops were used in a survey of 211 nests. Loegering (1992), however, experienced catastrophic nest loss in Maryland when six of seven topless exclosures were depredated by unidentified avian predators. I believe that the risk of abandonment at topped exclosures is outweighed by the risk of avian predation at topless nests. I frequently observed piping plovers mobbing avian predators in tern-like fashion emphasizing the existing threat imposed on piping plover nests.

Notably, lowest single year productivity (0.57) in this study occurred in 1990 when most egg loss at exclosed nests (45.0%) was attributed to flooding in an extremely wet nesting season. But flooding is largely a chance occurrence outside of management control (with some exceptions) and piping plovers have mechanisms (ie. re-nesting) to compensate for flood losses. Predator pressure, however, remains consistent or increases through re-nesting, causing more severe and permanent losses to productivity (especially when adult

plovers are depredated; A. Hecht, pers. comm.) unless effective management control is applied.

Lowering predator pressure through lethal trapping is difficult when no barriers exist to curtail immigration. Where physiogeographically feasible (e.g. peninsulas or sparsely vegetated beaches and impoundments) electric fences may provide effective egg protection. Fences may be especially appropriate for high density nesting areas where many nests would profit from fencing of relatively small, easily maintained areas.

Using electric fencing to protect piping plover nests in North Dakota, Mayer and Ryan (1991) observed 71.0% greater nest survival at fenced beaches than at unfenced control sites over three years. Forster (1975) increased the size of a sandwich tern (Sterna sandvicensis) colony in England from 80 pairs to 450 pairs in one year by using electric fencing to prevent red foxes from depredating eggs. The need for lethal control of mammalian predators would be greatly reduced via electric fencing but trapping would still be necessary to remove mammalian predators that may overcome fenced boundaries and become established within the enclosed areas.

I found that increasing our trapping effort for red foxes did not result in corresponding increases in harvest. I did, however, capture more animals before piping plovers began nesting in 1990 and 1991 by initiating the trapping season progressively earlier each year. Preventing red foxes from

denning and reproducing appears to be the most effective strategy for controlling the population and affording protection to nesting piping plovers.

Anthony et al. (1991) observed dramatic improvement in the nesting success of black brant (Branta bernicla nigricans) after the removal of arctic foxes (Alopex lagopus) from their study site in Alaska. They concluded that high nesting success when fox predation was low indicated that other predators had only minor impact on productivity of brant.

If red foxes are the major predator of piping plover nests and chicks at Chincoteague NWR, nesting success should improve with a decrease in the fox population. Nesting success, however did not improve substantially with the increased harvest of red foxes. It is likely that I did not lower the red fox population sufficiently to improve nesting success or that the impact of other predators increased during the decrease in red fox abundance. Sargeant and Sovoda (1990) found that in spite of a strong effort by experienced trappers to remove mammalian predators from their study sites in Minnesota and North Dakota, there was no significant improvement in nesting success of ducks. They concluded that the number of predators removed is not a valid gauge of the effectiveness of predator removal programs. Further, A. Sargeant (pers. comm.) indicated that predator removal must be thorough in order to be successful.

Increased effort in the removal of raccoons resulted in a significant increase in harvest of raccoons in this study, perhaps due in part to their willingness to enter live-catch traps. Patterson et al. (1991a) observed 11 of 14 piping plover nests on the Wild Beach depredated by raccoons in 1987. However, predator exclosures were not used in that study and may have prevented nest losses to raccoons. I observed no egg loss to raccoons at exclosed nests and only one un-exclosed nest was lost to a raccoon (n = 3 yrs.). Although I believe trapping and predator exclosures were successful in the protection of piping plover eggs from raccoons, raccoons may have been responsible for a substantial portion of chick loss, especially on the Wild Beach. Red foxes travelled freely between the Wild Beach and the Wash Flats and both red foxes and raccoons were removed from all three nesting areas.

Ghost crabs inhabit sandy beaches from Rhode Island to Brazil (Rathbun 1918, Christophers 1986). Their burrows can be found from just above the high tide line to as much as a quarter of a mile inland (Diaz and Costlow 1972). Steiner and Leatherman (1981) found that ghost crab densities varied significantly from site to site and between dates on Assateague Island. In this study ghost crab populations on the Wild Beach appear to be increasing each year and within years with later date in the season. Although I did not survey ghost crabs on other beaches at Chincoteague NWR, Steiner and Leatherman (1981) found significantly lower ghost crab

densities on beaches where ORV traffic was present. Wolcott and Wolcott (1984) found that ghost crabs were protected from ORV traffic by burrows as shallow as 5 cm but that large numbers of ghost crabs were killed by ORV traffic at night while they were feeding on the foreshore.

Ghost crab densities on the Wild Beach are much higher than observed at beaches in North Carolina (T. Wolcott pers. comm.) and piping plover populations are also higher in Virginia than in North Carolina. Assateague Island may represent a unique situation on the Atlantic Coast where both species exist and interact in relatively high numbers. Christophers (1986) observed that ghost crabs on Assateague feed primarily on mole crabs (Emerita talpoida) which are abundant from May through November. Wolcott (1978) found that clams (Donax sp.) were also an important food source for ghost crabs in North Carolina.

Other researchers on Assateague Island (Patterson 1988, Loegering 1992) have observed piping plovers defending chicks from ghost crabs and Loegering was able to confirm predation of a single chick by a ghost crab in Maryland. Although I was not able to observe predation of chicks by ghost crabs, I believe that the frequently observed defensive behaviors of adult piping plovers and the absence of evidence of other predators in many cases suggests that ghost crabs are a significant source of piping plover chick loss. Further, fledging rates are lowest for piping plovers on the Wild Beach

where ghost crab population density is highest at Chincoteague NWR. Piping plover chicks may be susceptible to predation by ghost crabs on the Wild Beach if food for young piping plovers is limited to the intertidal surf zone forcing chicks to cross open beaches where crabs are abundant and active on warm summer days.

Although indirect evidence is strong, insufficient information is presently available to determine the actual cause of high chick mortality on the Wild Beach. Wolcott and Wolcott (1994) observed no predation of piping plover chicks by ghost crabs in 116 hrs. of direct observation at Chincoteague NWR. They concluded that two sources of mortality exist: predation and poor nutrition, with poor nutrition accounting for most of the mortality after the first day for chicks. I concur that nutrition may play an important role in chick survival on the Wild Beach due to the unavailability or inaccessibility of suitable foraging areas. However, I believe it probably functions by weakening chicks making them more vulnerable to ghost crabs and other predators. Chick survival on the Wild Beach, then, is limited by both nutrition and predation.

PART 3. NESTING HABITAT SELECTION AND UTILIZATION

Piping plovers are biparental, principally monogamous shorebirds (Haig and Oring 1988b). In their Atlantic coast breeding range, they nest primarily on highly dynamic oceanfront beaches (Cairns 1982, Golder and Parnell 1987, Strauss 1989, USFWS 1988, 1988d, Whyte 1985). Nest scrapes for piping plovers are simple depressions in the sand, often lined with pebbles or bits of broken shells (Johnsgard 1984, USFWS 1988). As ground nesters, piping plover nesting success can be strongly limited by weather forces and by predators.

Selection of general macrohabitats, breeding territories, and microhabitats within the oceanfront landscape can play a role in reproductive success by influencing mate selection, prey availability and nest protection (Burger 1987). Further, the non-random dispersion of nests within space may result from a direct response to features of the environment as well as to the presence or absence of conspecifics (Brown and Orians 1970). Dispersion of individuals and their breeding territories may affect nesting success and population dynamics by influencing anti-predator behaviors and by limiting the number of individuals that an environment can support. Although piping plovers are generally thought of as solitary

nesters, their nests are sometimes aggregated in semi-colonial fashion (Haig 1992). The density of nesting pairs may determine nest defense strategies, resulting in subsequent variation in reproductive success.

Direct habitat loss due to anthropogenic effects throughout the piping plover's Atlantic coast range may be amplified if intraspecific social interactions limit piping plover population size or if suboptimal nesting habitats are selected due to the unavailability of optimal ones.

In this chapter, I report data regarding habitat availability and habitat selection as well as correlates of habitat quality and nesting success. I also analyze estimates of dispersion of nest sites for suggestions of spatial limitation due to social interactions. Finally, I characterize nest sites according to macrohabitat and microhabitat and examine the effects of differing nesting densities on reproductive success.

METHODS

I measured the availability of piping plover nesting habitat from 1:500 scale maps constructed from latitude and longitude coordinates (degrees, minutes, hundredths of minutes) generated from a portable LORAN C navigational computer (Micrologic Explorer) with battery pack. The LORAN C system was designed for marine navigation but also has proven

applications for accurate recording of wildlife locations, landmarks, and permanent sample plots (Patric et al 1988). LORAN coordinates were collected from a vehicle or on foot at 0.16 km intervals along the borders of suitable nesting habitat in each of the three major nesting areas (Hook, Wild Beach, Wash Flats) at Chincoteague National Wildlife Refuge in the summer of 1989. Suitable nesting habitat borders were assessed in the field as an oceanfront wrack, other water barrier, secondary or tertiary dune line, or continuous vegetational barrier. Large areas of water formed by rain or tides were also mapped and subtracted from the total area of suitable nesting habitat.

All Loran coordinates were plotted on 78.7 cm^2 graph paper. An equivalency of 0.01 minutes of latitude or longitude to 50 ft. resulted in the 1:500 scale. Areas of available nesting habitat were calculated from the maps by counting the number of 2500 $ft.^2$ squares within habitat borders and converting to hectares. Squares falling on the edge of habitat borders were included if 50% of the square was within the border and excluded if 50% of the square was outside of the border. LORAN C coordinates were accurate to a mean of 34.4 m. I used 110 LORAN C coordinates to map nesting habitat on the Hook, 86 for the Wild Beach, and 43 for the Wash Flats.

At each piping plover nest, I measured the distance to oceanfront wrack, bayside marsh, mudflat, or vegetational barrier, tidal pool, least tern nest (within 300 ft., 1989

only) and total beach width. Nonparametric statistics were then used to detect significant differences between successful nests and unsuccessful nests (hatching success and fledging success) for each year according to temporal, physical, and social categories of nesting.

I allocated all nests into one of eight categories of macrohabitat type (berm, foredune, backdune, dune, overwash, blowout, flats, tump). Hatching success was then examined in each year according to macrohabitat type to determine the influence of nest location.

Measurements of microhabitats at piping plovers nests recorded in this study include nest height, shell cover, and vegetation cover. A row by column test of independence using G test (Sokal and Rolfe 1981) was used to determine if selection of high or low nest sites was associated with the timing of nest initiation within the season in 1989. I hypothesized that early nesters might select higher nest sites less vulnerable to flooding. I used a line level and graduated poles to measure the height of piping plover nests along a transect perpendicular to beach length. Transects were 40 m long with the nest at the center. All measurements were taken after the nest had failed or the eggs had hatched to avoid disturbance to birds. Nests were considered "high" if they were above the midpoint of elevation along the transect and "low" if they were below the midpoint. Nests were considered "early" if they were initiated prior to 13 May and "late" if

initiated after 13 May. Shell cover and vegetation cover at piping plover nests were estimated in 1990 as indicators of nest concealment. Both measures were collected by observing a 1 m^2 grid with the nest at the center and estimating the percent of the grid obscured by shells and vegetation.

Spatial patterns of piping plover nests were determined using a nearest neighbor analysis (Clark and Evans 1954). Nest spacing was categorized as random, regular or clumped. Resulting R statistics were tested for departure from random using a t-test.

I divided nest locations on the Hook and the Wild Beach into two broad physical categories for analysis based on their proximity to oceanfront or bayside habitat borders. Inner beach nests are closer to bayside habitat borders than to oceanfront wrack. Outer beach nests are closer to oceanfront wrack than to bayside habitat borders.

A Shannon type Index of Diversity (Zar 1974, Magurran 1988) was used to determine the degree of nest site diversity between inner and outer categories, that is, the likelihood of either habitat being selected instead of the other. This index is appropriate for nominal scale data where no mean or median is available to evaluate dispersion. The quantitative index expression (H) is influenced not only by diversity but also by the number of categories. Therefore, an adjustment is made to express the observed diversity as J, a proportion of the maximum possible diversity. J can range in value from 0.0 to

1.0, with a small J indicating low diversity of nest locations and a large J indicating high diversity. A t-test was used to test for significant differences in relative diversity of nest locations between the Hook and the Wild Beach and between each nesting area compared to the relative diversity of all nest sites.

I further examined inner beach and outer beach habitat categories using Utilization/Availability testing (Neu 1974) to detect distinct preference or avoidance of either nesting habitat category. G tests were first employed to compare the observed frequency versus the expected frequency of nest locations in either category. Hypothesis testing was based on the use of each habitat in exact proportion to its availability. Expected frequencies were calculated by multiplying the number of nests in each area by the percentage of habitat available in each habitat category. Inner beach and outer beach habitats were equally available on the Hook and on the Wild Beach. On the Wash Flats, however, nests within 100 m of a continuous habitat border were considered as inner nests. Nests that were greater than 100 m but less than 1000 m from a continuous habitat were considered as outer nests. This resulted in a 9:1 ratio of availability of outer habitats to inner habitats on the Wash Flats.

If G tests were significant, then Utilization/Availability testing could proceed. This method establishes 95% confidence intervals around observed

proportions of nest locations and compares them to the expected proportion.

Semi-colonial nesting, as opposed to nesting in isolation, may be a response to gradients of nesting habitat quality or to patchiness of food resources or to some other variable. High density nesting, however, may promote nest defense strategies that differ from crypsis and spacing out of nests relied on in low density nesting situations. Reproductive advantages may be realized in semi-colonial nesting areas if resources are not limiting and/or if antipredator strategies are more effective. I calculated nesting density as the number of nests per km of nesting habitat for all three years in the three major nesting areas and in two sub-categories of nesting habitat on the Hook. I then calculated the percentage of nests depredated, eggs hatched, and young fledged for the same areas. I compared parameters between high density and low density nesting areas. Differences between nesting areas were compared using ANOVA and the data was examined for trends between higher density and lower density nesting areas.

I also estimated the flushing distance (Pulliam and Mills 1977) whenever I encountered an incubating plover during daily nest checks. Flushing distances were used to determine minimum buffers necessary to allow undisturbed nesting and were compared between nesting areas and between years.

RESULTS

NEST SITE SELECTION

Piping plover nests (n = 129) were found in eight different habitat categories (Table 3.1) during this study. Overall, I found 41 nests (31.8%) on the beach berm, 10 nests (7.8%) on foredune slopes, 29 nests (22.5%) in backdune areas, 7 nests (5.4%) on dunes, 8 nests (6.2%) in blowouts, 6 nests (4.7%) in washovers, 25 nests (19.4%) on flats, and 4 nests (3.1%) on tumps. Habitat categories described as "flats" and "tumps" were found only on the Wash Flats. All other habitat categories were found to varying degrees on the Hook and the Wild Beach.

On the Hook, most nests (44.6%, n = 74) were found on the berm (Table 3.2) although the percentage of berm nests decreased each year. Only 28.0% of all Hook nests in 1991 (n = 25) were found on the berm. Piping plovers on the Hook showed an increasing tendency to nest in backdune areas, often within thick vegetation. Only 3 nests in 1989 (15.8%, n = 19) were found in backdune habitats on the Hook. But 14 nests (46.7%, n = 30) in 1990 and 9 nests (36.0%, n = 25) in 1991 were found in backdune habitats. Berm nesting habitats were used more than expected ($X^2 = 34.84$, $P < 0.001$, n = 74) on the Hook as were backdune habitats ($X^2 = 15.26$, $P < 0.001$, n = 26).

Table 3.1. Nesting Habitat Definitions.

Term	Definition
Berm	Dry, open, sandy beach between base of foredune and mean high water line (wrack); low, ephemeral dunes may be present; vegetation is generally sparse.
Foredune	Ocean-front slope of primary dunes; vegetation may be sparse or thick.
Backdune	Open areas behind unbroken primary dunes but not necessarily behind secondary dunes; may be wet (as barrier flats where rain water or tidal overwash remains standing temporarily) or may be dry and shelly; vegetation variable but increasing with distance from primary dunes.
Dune	Crest of primary or secondary dunes; vegetated in variable amounts.
Overwash	Area of beach regularly inundated by tidal flooding; vegetation sparse.
Blowout	Breaks in primary dune system caused by wind and/or tidal erosion; sparsely vegetated.
Flats	Drained fresh water or brackish water impoundment bottom; flat; unvegetated; may be easily flooded by rainwater.
Tump	Small mounds or ridges of sandy soil on open impoundment bottom (drained); vegetated with grasses or forbs.

Table 3.2. Nesting habitat types for piping plovers at Chincoteague NWR, 1989-1991.

Habitat Type		Hook			Wild Beach			Wash Flats		
		1989	1990	1991	1989	1990	1991	1989	1990	1991
Berm	No. Nests	13	13	7	3	3	2	0	0	0
	%	65.0	43.3	28.0	60.0	21.4	25.0	0.0	0.0	0.0
Foredune	No. Nests	2	1	1	2	4	0	0	0	0
	%	10.0	3.3	4.0	40.0	28.6	0.0	0.0	0.0	0.0
Backdune	No. Nests	3	14	9	0	1	2	0	0	0
	%	15.8	46.7	36.0	0.0	7.1	25.0	0.0	0.0	0.0
Dune	No. Nests	0	1	5	0	0	1	0	0	0
	%	0.0	3.3	20.0	0.0	0.0	12.5	0.0	0.0	0.0
Blowout	No. Nests	0	0	2	0	3	3	0	0	0
	%	0.0	0.0	8.0	0.0	21.4	37.5	0.0	0.0	0.0
Overwash	No. Nests	1	1	1	0	3	0	0	0	0
	%	5.0	3.3	4.0	0.0	21.4	0.0	0.0	0.0	0.0
Flats	No. Nests	0	0	0	0	0	0	7	10	8
	%	0.0	0.0	0.0	0.0	0.0	0.0	100.0	100.0	60.0
Tump	No. Nests	0	0	0	0	0	0	0	0	4
	%	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	40.0

On the Wild Beach, more nests were found on the berm (30.77%, n = 26) than in any other habitat category but the difference was not significant ($X^2 = 3.18$, $P > 0.05$, n = 26). Piping plover nests on the Wash Flats were usually found on bare Flats (86.2%, n = 29) as opposed to vegetated tumps. Wash Flats piping plover nests were found more often than expected on bare flats ($X^2 = 7.60$, $P < 0.01$, n = 29) than on vegetated tumps.

Of 222 eggs produced at piping plover nests in 6 habitat categories on the Hook (Table 3.3), 104 (46.9%) were found in berm nests. Of 104 eggs found in berm nests, 56 (53.9%) hatched successfully. Piping plover eggs found in berm nests hatched significantly more often than expected in all three years of this study (1989, $X^2 = 7.08$, $P < 0.01$; 1990, $X^2 = 17.07$, $P < 0.001$; 1991, $X^2 = 6.55$, $P < 0.025$). Piping plover eggs in backdune, dune, overwash, and blowout habitat categories on the Hook did not differ significantly in hatching success from expected values. At foredune nests on the Hook, however, fewer eggs (0, n = 4) hatched than expected in the 1990 breeding season.

Eggs on the Wild Beach (Table 3.4) were found most often in berm nests also (28 eggs, 28.0%, n = 100). However, hatching success for eggs in berm nests on the Wild Beach was greater than expected only in 1990 ($X^2 = 10.0$, $P < 0.005$) and hatching success was lower than expected in 1989 ($X^2 = 4.0$, $P < 0.05$). Piping plovers selected more backdune nest sites on

the Wild Beach in each year of the study (0.0%, 4.0%, 8.0% respectively). Although only 12 eggs (12.0%) were found in backdune nests on the Wild Beach, they hatched more often than expected in 1990 ($X^2 = 4.0$, $P < 0.05$) and in 1991 ($X^2 = 5.0$, $P < 0.05$). No backdune nests were found on the Wild Beach in 1989. Piping plovers on the Wild Beach also exhibited a strong (24.0%, n = 100) and increasing (1989, 0.0%; 1990, 12.0%; 1991, 12.0%) tendency to lay eggs in nests in dune blowouts. Eggs in blowout nests, however, hatched less often (83.3% unhatched) than expected in 1990 ($X^2 = 5.33$, $P < 0.025$).

Eighty-seven eggs (87.0%, n = 100) found on the Wash Flats were found in nests on the bare flats (Table 3.5). In 1991, fewer eggs hatched (23.3%, n = 30) than expected from nests found on flats ($X^2 = 8.53$, $P < 0.005$). This may have been due to accelerated nest abandonment rates observed, especially on the Wash Flats, in that year. However, also in 1991, I noted a shift in some Wash Flats nesters (30.2%, n = 43 eggs) to tumps for nesting habitat. Eggs laid in tump nests, however, did not hatch significantly more often than expected ($X^2 = 1.92$, $P > 0.05$).

I observed a mean beach width of 146.2 ± 86.1 m at 99 piping plover nests in oceanfront habitats on the Hook and the Wild Beach from 1989 to 1991. Beach width ranged from 20.4 m to 332.5 m. Beach width was not an appropriate measurement for habitat on the Wash Flats. Mean beach width was greater at piping plover nests on the Hook (176.0 ± 81.4 m, n = 70) than

Table 3.3. Distribution of piping plover eggs on the Hook according to habitat type and success.

Hook Habitat Type	1989 Egg Fate			1990 Egg Fate			1991 Egg Fate		
	Total	Hatched	Failed	Total	Hatched	Failed	Total	Hatched	Failed
Berm	51 obs.	35	16	31 obs.	4	27	22 obs.	17	5
	exp.	25.5	25.5	exp.	15.5	15.5	exp.	11.0	11.0
X^2		7.0784			17.0645			6.5455	
		P < 0.01			P < 0.001			P < 0.025	
Foredune	8 obs.	6	2	4 obs.	0	4	1 obs.	0	1
	exp.	4.0	4.0	exp.	2.0	2.0	exp.	0.5	0.5
X^2		2.0000			4.0000			1.0000	
		P > 0.05			P < 0.05			P > 0.05	
Backdune	12 obs.	4	8	40 obs.	19	21	31 obs.	13	18
	exp.	6.0	6.0	exp.	20.0	20.0	exp.	15.5	15.5
X^2		1.3333			0.1000			0.8065	
		P > 0.05			P > 0.05			P > 0.05	
Dune	0 obs.	0	0	3 obs.	2	1	4 obs.	3	1
	exp.	0.0	0.0	exp.	1.5	1.5	exp.	2.0	2.0
X^2					0.3333			1.0000	
					P > 0.05			P > 0.05	

Table 3.3 (Continued).

Hook Habitat Type		1989 Egg Fate			1990 Egg Fate			1991 Egg Fate		
		Total	Hatched	Failed	Total	Hatched	Failed	Total	Hatched	Failed
Overwash		4 obs.	3	1	2 obs.	0	2	4 obs.	3	1
		exp.	2.0	2.0	exp.	1.0	1.0	exp.	2.0	2.0
	X^2		1.0000			2.0000			1.0000	
			P > 0.05			P > 0.05			P > 0.05	
Blowout		0 obs.	0	0	0 obs.	0	0	5 obs.	2	3
		exp.	0.0	0.0	exp.	0.0	0.0	exp.	2.5	2.5
	X^2								2.0000	
									P > 0.05	

Table 3.4. Distribution of piping plover eggs on the Wild Beach according to habitat type and success.

Wild Beach Habitat Type	1989 Egg Fate				1990 Egg Fate				1991 Egg Fate			
	Total		Hatched	Failed	Total		Hatched	Failed	Total		Hatched	Failed
Berm	10	obs.	4	6	10	obs.	10	0	8	obs.	7	1
		exp.	5	5		exp.	5	5		exp.	4	4
X^2			4.000				10.000				4.500	
			P < 0.05				P < 0.005				P < 0.05	
Foredune	8	obs.	8	0	16	obs.	11	5	0	obs.	0	0
		exp.	4	4		exp.	8	8		exp.	0	0
X^2			8.000				2.250					
			P < 0.005				P > 0.05					
Backdune	0	obs.	0	0	4	obs.	4	0	8	obs.	5	3
		exp.	0	0		exp.	2	2			4	4
X^2							4.000				5.000	
							P < 0.05				P < 0.05	
Dune	0	obs.	0	0	0	obs.	0	0	4	obs.	4	0
		exp.	0	0		exp.	0	0		exp.	2	2
X^2											4.000	
											P < 0.05	

Table 3.4 (Continued).

Wild Beach Habitat Type	1989 Egg Fate			1990 Egg Fate			1991 Egg Fate		
	Total	Hatched	Failed	Total	Hatched	Failed	Total	Hatched	Failed
Overwash	0 obs.	0	0	8 obs.	4	4	0 obs.	0	0
	exp.	0	0	exp.	2	2	exp.	0	0
X^2					0.000				
					P > 0.05				
Blowout	0 obs.	0	0	12 obs.	2	10	12 obs.	7	5
	exp.	0	0	exp.	6	6	exp.	6	6
X^2					5.333			0.333	
					P < 0.025			P > 0.05	

Table 3.5. Distribution of piping plover eggs on the Wash Flats according to habitat type and success.

Wash Flats Habitat Type	1989 Egg Fate			1990 Egg Fate			1991 Egg Fate		
	Total	Hatched	Failed	Total	Hatched	Failed	Total	Hatched	Failed
Flats	23 obs.	14	9	34 obs.	19	15	30 obs.	7	23
	exp.	11.5	11.5	exp.	17	17	exp.	15	15
X^2		1.087			0.471			8.533	
		P > 0.05			P > 0.05			P < 0.005	
Tump	0 obs.	0	0	0 obs.	0	0	13 obs.	4	9
	exp.	0	0	exp.	0	0	exp.	6.5	6.5
X^2								1.923	
								P > 0.05	

on the Wild Beach (66.7 ± 31.2, n = 29) and the difference was significant (F = 45.87, P < 0.001, df=1,98).

Piping plovers nested significantly closer to the oceanfront wrackline on the Wild Beach (mean = 51.9 ± 22.8 m, n = 27, range = 16.2 - 91.8 m) than they did on the Hook (mean = 123.4 ± 60.3 m, n = 72, range = 13.4 - 296.6 m)(F = 35.74, P < 0.001, df = 1,97). On the Wash Flats piping plover nests ranged from 3.1 - 259.4 m (mean = 71.6 ± 60.2 m, n = 27) from a continuous vegetation barrier on the east side of the impoundment.

Physical factors of nest site selection including (1) distance to ocean, (2) distance to habitat barriers, and (3) total beach width, did not appear significant to the subsequent hatching success or fledging success of piping plovers nesting on the Hook and the Wild Beach (Tables 3.6 - 3.11). Two exceptions occurred in 1990 (Table 3.7) when unsuccessful egg clutches were farther from the ocean (104.4 ± 58.4 m) than successful ones (91.0 ± 62.9 m) (Wilcoxon two-sample Rank Sum test, P = 0.0355) and beach width was greater at unsuccessful nests (177.4 ± 75.5 m) than at successful ones (126.2 ± 78.9 m)(Wilcoxan two-sample Rank Sum test, P = 0.0213). This is probably due to an extremely wet nesting season in 1990 when egg losses were high due to flooding in all nesting areas.

Social factors examined included (1) the number of pairs that a given pair of piping plovers nested with in the same

nesting area and (2) the distance to a nearest conspecific neighbor. These factors were examined according to hatching success (Tables 3.6 - 3.8) and fledging success (Tables 3.9 - 3.11). Significant results were observed only in 1990 (Table 3.7) when hatching success and nesting density (no. pairs) were inversely related. Successfully hatched clutches occurred where significantly fewer birds (15.5 ± 6.8 pairs) nested in a nesting area in contrast to areas with more birds (19.6 ± 6.1 pairs)(Wilcoxan two-sample Rank Sum test, P = 0.0169). Nesting density, expressed as no. of pairs or nesting dispersion expressed as nearest neighbor distance, did not have a significant influence on fledging success in these comparisons.

Seasonal timing of clutch initiation appears to play a role in hatching success and fledging success although the results were variable. In 1989 and 1991 the clutch initiation date was not a significant factor in hatching success (Table 3.6 and 3.8). In 1990 (Table 3.7) clutch initiation date was significantly later (31 May ± 22 days) at successful nests than at unsuccessful nests (15 May ± 17 days)(Wilcoxan two-sample Rank Sum test, P = 0.0094). Fledging success was significantly influenced by clutch initiation date only in 1989 (Table 3.9). In that year, the clutch initiation date was earlier (5 May ± 13 days) at nests that fledged young than at nests that did not fledge young (22 May ± 19 days)(Wilcoxon two-sample Rank Sum test, P = 0.0118).

Table 3.6. Comparisons of piping plover nests hatching no eggs (unsuccessful) and those hatching 1 or more eggs (successful), 1989. Given are means ± standard deviations.

Category	Hatching Success 1989 Successful Nests	Unsuccessful Nests	Probability [1]
Number of Nests	31	5	
Clutch Size	3.55 ± 0.77	3.60 ± 0.89	P=0.7711
Number of Eggs Hatched	3.16 ± 0.78	0	
Number of Exclosures	23	4	
Temporal Factors			
Clutch Initiation Date	16 May ± 19 days	17 May ± 12 days	P=0.8494
Clutch Initiation Date (relative to mean) [2]	-0.36 ± 18.69	1.75 ± 19.47	P=0.5266
Physical Factors (n = 24,4, Hook and Wild Beach only)			
Distance to Ocean [3]	111.8 ± 61.3	104.6 ± 119.6	P=0.7150
Distance to Barrier [4]	63.6 ± 49.6	14.3 ± 7.6	P=0.0828
Beach Width	173.9 ± 99.8	118.9 ± 113.8	P=0.4113
Tidal Pool Present [5]	12	2	
Social Factors			
No. Pairs [6]	18.7 ± 12.7	20.0 ± 13.7	P=0.8386
Nearest Neighbor [7]	192.3 ± 169.5	263.8 ± 165.0	P=0.2536
Tern Nest Present [8]	11	1	

[1] Wilcoxon two-sample Rank Sum test
[2] Date of clutch initiation for each nest relative to the mean date of clutch initiation in its nesting area (Hook, Wild Beach, Wash Flats). A negative number indicates that nests were initiated prior to the mean clutch initiation date.
[3] Distance (m) to mean high tide (wrack).
[4] Habitat barriers include marshes, mud flats, water, dense vegetation or other features that delimit nesting habitat (m).
[5] Tidal pool within 100 m.
[6] Number of pairs in the nesting area.
[7] Nearest piping plover nest (m)
[8] Least tern nest within 100 m

Table 3.7. Comparisons of piping plover nests hatching no eggs (unsuccessful) and those hatching 1 or more eggs (successful), 1990. Given are means ± standard deviations.

Category	Hatching Success 1990 Successful Nests	Unsuccessful Nests	Probability [1]
Number of Nests	32	27	
Clutch Size	3.25 ±0.92	2.78 ± 1.25	P=0.1878
Number of Eggs Hatched	3.03 ± 0.90	0	
Number of Exclosures	23	14	
Temporal Factors			
Clutch Initiation Date	31 May ± 22 days	15 May ± 17 days	P=0.0094**
Clutch Initiation Date (relative to mean) [2]	7.47 ± 20.20	-6.46 ± 17.80	P=0.0101**
Physical Factors (n = 20,24, Hook and Wild Beach only)			
Distance to Ocean [3]	91.0 ± 62.9	104.4 ± 58.4	P=0.03546*
Distance to Barrier [4]	35.2 ± 41.6	73.6 ± 71.4	P=0.1160
Beach Width	126.2 ± 78.9	177.4 ± 75.5	P=0.0213*
Social Factors			
No. Pairs [5]	15.5 ± 6.8	19.6 ± 6.1	P=0.0169*
Nearest Neighbor [6]	223.4 ± 189.5	187.6 ± 163.7	P=0.3403

[1] Wilcoxon two-sample Rank Sum test
[2] Date of clutch initiation for each nest relative to the mean date of clutch initiation in its nesting area (Hook, Wild Beach, Wash Flats). A negative number indicates that nests were initiated prior to the mean clutch initiation date.
[3] Distance (m) to mean high tide (wrack).
[4] Habitat barriers include marshes, mud flats, water, dense vegetation or other features that delimit nesting habitat (m).
[5] Number of pairs in the nesting area.
[6] Nearest piping plover nest (m)

Table 3.8. Comparisons of piping plover nests hatching no eggs (unsuccessful) and those hatching 1 or more eggs (successful), 1991. Given are means ± standard deviations.

Category	Hatching Success 1991 Successful Nests	Unsuccessful Nests	Probability [1]
Number of Nests	28	18	
Clutch Size	3.61 ± 0.74	3.22 ± 1.06	P=0.2005
Number of Eggs Hatched	3.39 ± 0.99	0	
Number of Exclosures	27	13	
Temporal Factors			
Clutch Initiation Date	14 May ± 13 days	24 May ± 17 days	P=0.0759
Clutch Initiation Date (relative to mean) [2]	-4.16 ± 11.75	4.55 ± 16.40	P=0.1107
Physical Factors (n = 21,8, Hook and Wild Beach only)			
Distance to Ocean [3]	105.9 ± 58.1	116.3 ± 72.0	P=0.7772
Distance to Barrier [4]	43.2 ± 59.0	46.6 ± 47.8	P=0.5440
Beach Width	107.5 ± 74.8	144.7 ± 92.0	P=0.4071
Social Factors			
No. Pairs [5]	14.2 ± 4.9	12.9 ± 4.7	P=0.8712
Nearest Neighbor [6]	288.1 ± 253.7	278.9 ± 431.8	P=0.1859

[1] Wilcoxon two-sample Rank Sum test
[2] Date of clutch initiation for each nest relative to the mean date of clutch initiation in its nesting area (Hook, Wild Beach, Wash Flats). A negative number indicates that nests were initiated prior to the mean clutch initiation date.
[3] Distance (m) to mean high tide (wrack).
[4] Habitat barriers include marshes, mud flats, water, dense vegetation or other features that delimit nesting habitat (m).
[5] Number of pairs in the nesting area.
[6] Nearest piping plover nest (m)

Table 3.9. Comparisons of piping plover nests fledging no chicks (unsuccessful) and those fledging 1 or more chicks (successful), 1989. Given are means ± standard deviations.

Category	Fledging Success 1989 Successful Nests	Unsuccessful Nests	Probability [1]
Number of Nests	16	20	
Clutch Size	3.38 ± 0.89	3.70 ± 0.66	P=0.2243
Number of Chicks Fledged	2.06 ± 7.81	0	
Number of Exclosures	10	17	
Temporal Factors			
Clutch Initiation Date	5 May ± 13 days	22 May ± 19 days	P=0.0118**
Clutch Initiation Date (relative to mean) [2]	-9.64 ± 13.40	5.78 ± 18.97	P=0.0171*
Physical Factors (n = 12,16, Hook and Wild Beach only)			
Distance to Ocean [3]	113.6 ± 65.7	109.1 ± 71.0	P=0.8011
Distance to Barrier [4]	63.9 ± 44.8	52.8 ± 52.9	P=0.4309
Beach Width	177.5 ± 95.8	159.8 ± 106.7	P=0.7055
Tidal Pool Present [5]	8	6	
Social Factors			
No. Pairs [6]	19.1 ± 12.8	18.7 ± 12.8	P=0.8316
Nearest Neighbor [7]	163.0 ± 129.4	228.1 ± 186.1	P=0.2628
Tern Nest Present [8]	6	6	

[1] Wilcoxon two-sample Rank Sum test
[2] Date of clutch initiation for each nest relative to the mean date of clutch initiation in its nesting area (Hook, Wild Beach, Wash Flats). A negative number indicates that nests were initiated prior to the mean clutch initiation date.
[3] Distance (m) to mean high tide (wrack).
[4] Habitat barriers include marshes, mud flats, water, dense vegetation or other features that delimit nesting habitat (m).
[5] Tidal pool within 100 m
[6] Number of pairs in the nesting area.
[7] Nearest piping plover nest (m)
[8] Least tern nest within 100 m

Table 3.10. Comparisons of piping plover nests fledging no chicks (unsuccessful) and those fledging 1 or more chicks (successful), 1990. Given are means ± standard deviations.

Category	Fledging Success 1990 Successful Nests	Unsuccessful Nests	Probability [1]
Number of Nests	16	43	
Clutch Size	3.19 ± 0.91	2.98 ± 1.65	P=0.7155
Number of Chicks Fledged	1.50 ± 0.63	0	
Number of Exclosures	10	27	
Temporal Factors			
Clutch Initiation Date	2 June ± 27 days	20 May ± 18 days	P=0.1299
Clutch Initiation Date (relative to mean) [2]	9.88 ± 23.88	-2.07 ± 17.92	P=0.0965
Physical Factors (n = 9,35, Hook and Wild Beach only)			
Distance to Ocean [3]	115.2 ± 83.1	93.3 ± 53.2	P=0.5403
Distance to Barrier [4]	27.2 ± 34.6	63.3 ± 65.6	P=0.1035
Beach Width	142.4 ± 91.3	156.6 ± 78.6	P=0.6221
Social Factors			
No. Pairs [5]	17.5 ± 7.6	17.4 ± 6.5	P=0.8638
Nearest Neighbor [6]	170.8 ± 87.2	213.2 ± 191.7	P=0.8927

[1] Wilcoxon two-sample Rank Sum test
[2] Date of clutch initiation for each nest relative to the mean date of clutch initiation in its nesting area (Hook, Wild Beach, Wash Flats). A negative number indicates that nests were initiated prior to the mean clutch initiation date.
[3] Distance (m) to mean high tide (wrack).
[4] Habitat barriers include marshes, mud flats, water, dense vegetation or other features that delimit nesting habitat (m).
[5] Number of pairs in the nesting area.
[6] Nearest piping plover nest (m)

Table 3.11. Comparisons of piping plover nests fledging no chicks (unsuccessful) and those fledging 1 or more chicks (successful), 1991. Given are means ± standard deviations.

Category	Fledging Success 1991 Successful Nests	Unsuccessful Nests	Probability [1]
Number of Nests	16	30	
Clutch Size	3.69 ± 0.50	3.33 ± 1.03	P=0.8216
Number of Chicks Fledged	1.88 ± 1.09	0	
Number of Exclosures	16	25	
Temporal Factors			
Clutch Initiation Date	13 May ± 14 days	19 May ± 15 days	P=0.8704
Clutch Initiation Date (relative to mean) [2]	-5.44 ± 14.10	1.09 ± 12.91	P=0.5925
Physical Factors (n = 13,16, Hook and Wild Beach only)			
Distance to Ocean [3]	99.6 ± 59.2	114.6 ± 63.2	P=0.6096
Distance to Barrier [4]	53.9 ± 67.6	37.7 ± 46.7	P=0.7450
Beach Width	121.0 ± 84.3	115.4 ± 79.5	P=0.8828
Social Factors			
No. Pairs [5]	14.4 ± 4.8	13.3 ± 4.8	P=0.7220
Nearest Neighbor [6]	306.1 ± 301.8	272.3 ± 353.2	P=0.8704

[1] Wilcoxon two-sample Rank Sum test
[2] Date of clutch initiation for each nest relative to the mean date of clutch initiation in its nesting area (Hook, Wild Beach, Wash Flats). A negative number indicates that nests were initiated prior to the mean clutch initiation date.
[3] Distance (m) to mean high tide (wrack).
[4] Habitat barriers include marshes, mud flats, water, dense vegetation or other features that delimit nesting habitat (m).
[5] Number of pairs in the nesting area.
[6] Nearest piping plover nest (m)

In 1989, I measured beach slope at 23 piping plover nests on the Hook and the Wild Beach (Table 3.12). No association was observed between the relative height of the nest and the timing of clutch initiation. Early nesting plovers, presumed to select the choicest nest sites, did not select higher nest sites significantly more often than lower ones ($G = 0.33$, $0.9 < P < 0.5$).

Piping plovers may have responded to predator pressure in 1991 by selecting more concealed nest sites. In 1990, mean percent vegetation cover was 11.4% (SE = 3.69, n = 29) at nests on the Hook and 1.1% (SE = 1.07, n = 14) at nests on the Wild Beach (Figure 3.1). In 1991, the mean percent vegetation cover was higher in both areas (Hook, mean = 28.2%, SE = 6.47, n = 25; Wild Beach, mean = 13.1%, SE = 10.0, n = 8)(Figure 3.2). The difference between years was significant on the Hook (two-sample t-test, $t = 2.26$, $P = 0.030$) but not on the Wild Beach (two-sample t-test, $t = 1.19$, $P = 0.270$). Better nest concealment may have led to better nest success on the Hook. In 1990, hatching success (no. eggs hatched/nest) and vegetation cover were positively correlated ($r = 0.569$, $P < 0.01$), but a similar test in 1991 showed no significant correlation ($r = -0.142$, $P > 0.05$).

Nests on the Hook had greater coverage by shell fragments (mean = 18.3%, SE = 3.30, n = 29) than nests on the Wild Beach (mean = 11.8%, SE = 3.29, n = 14) in 1990 (Figure 3.3). But, in 1991, Wild Beach nests had greater shell coverage (mean =

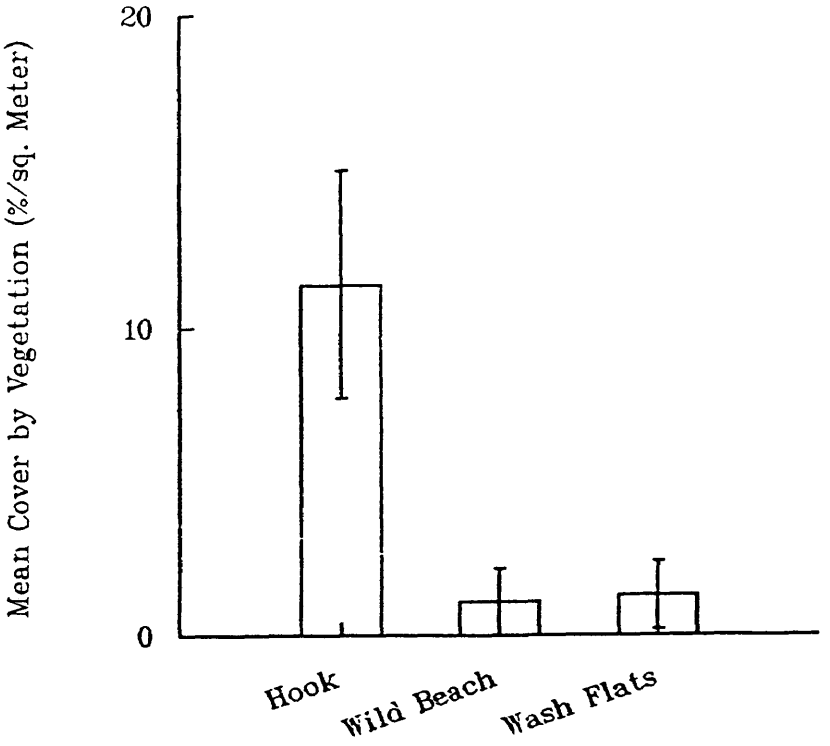
Table 3.12. RxC test of independence using G test. Frequencies of piping plover nest heights[1] for clutches initiated early vs late[2] in the breeding season at Chincoteague NWR, 1989.

Nest Height	Clutch Initiation Early	Late	Total (N)	% Early	G[3]	P
Low	5	6	11	45.5		
High	4	8	12	50.0	0.33	0.9<P<0.5
Total	9	14	23	39.1		

[1] See text for procedure of determining high vs low nests.
[2] Early nests initiated prior to 13 May. Late nests initiated on or after 13 May.
[3] G adjusted by Williams correction for RxC tables.

Figure 3.1. Mean coverage by vegetation at piping plover nests on the Hook, Wild Beach, and Wash Flats in 1990. Coverage was estimated to the nearest five percent from standing height with the nest at the center of a 1 m^2 grid. Sample sizes; Hook = 29, Wild Beach = 14, Wash Flats = 9. Error bars = SE.

Figure 3.2. Mean coverage by vegetation at piping plover nests on the Hook and Wild Beach in 1991. Coverage was estimated to the nearest five percent from standing height with the nest at the center of a 1 m^2 grid. Sample sizes; Hook = 25, Wild Beach = 8. Error bars = SE.


Mean Cover by Vegetation (%/sq. Meter)
20
10
0
Hook
Wild Beach
Wash Flats

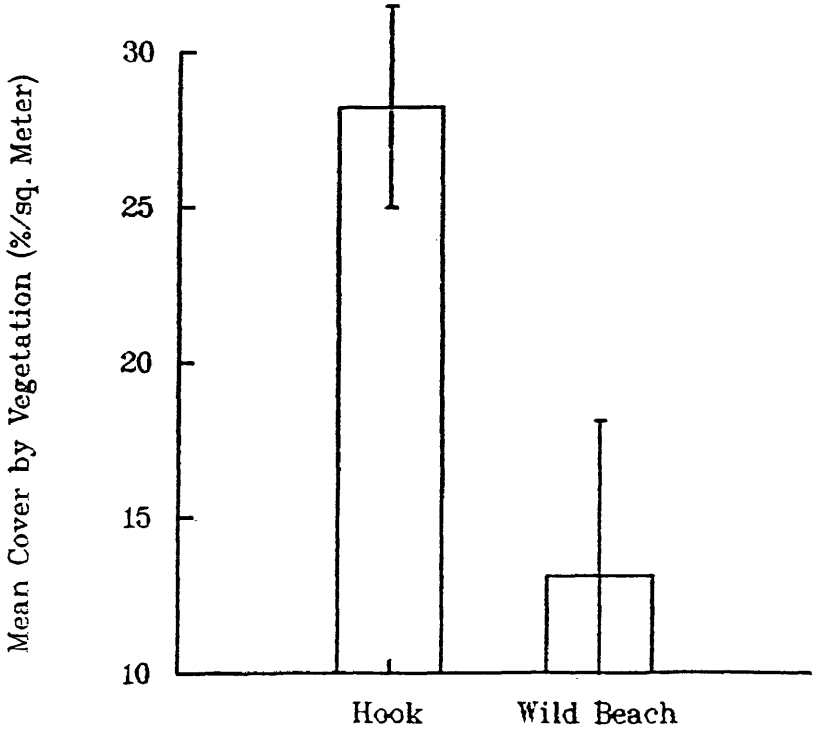
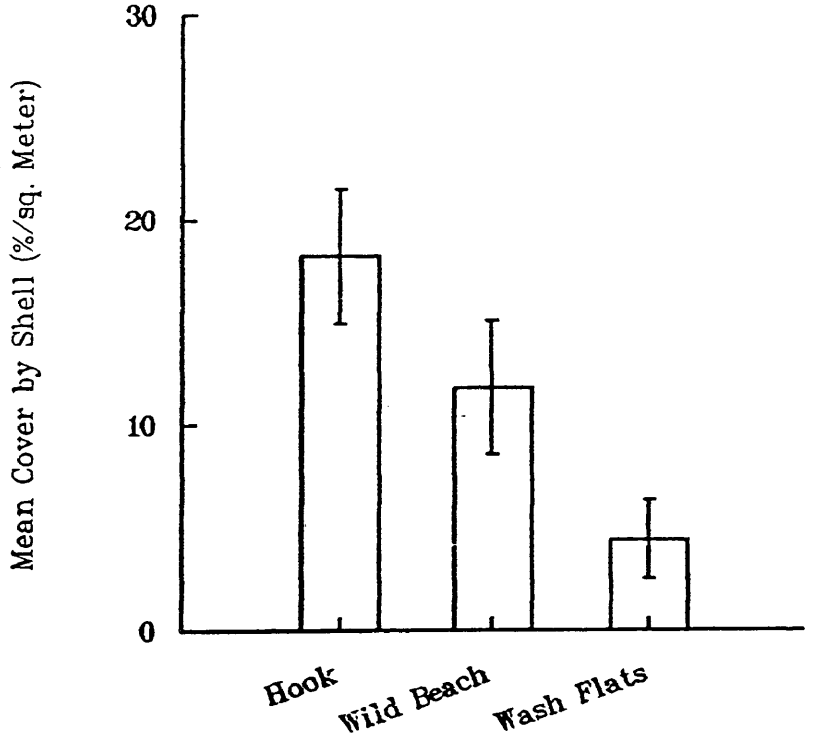
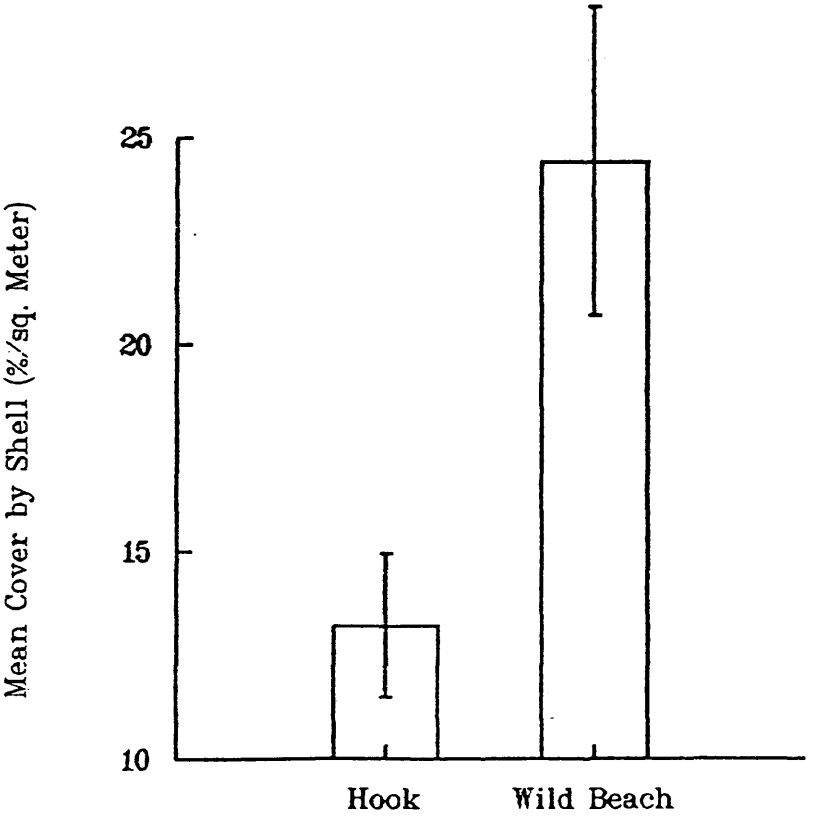

Mean Cover by Vegetation (%/sq. Meter)
30
25
20
15
10
Hook
Wild Beach

Figure 3.3. Mean coverage by shell fragments at piping plover nests on the Hook, Wild Beach, and Wash Flats in 1990. Coverage was estimated to the nearest five percent from a standing height with the nest at the center of a 1 m^2 grid. Sample sizes; Hook = 29, Wild Beach = 14, Wash Flats = 9. Error bars = SE.

Figure 3.4. Mean coverage by shell fragments at piping plover nests on the Hook and the Wild Beach in 1991. Coverage was estimated to the nearest five percent from standing height with the nest at the center of a 1 m^2 grid. Sample sizes; Hook = 25, Wild Beach = 8. Error bars = SE.


Mean Cover by Shell (%/sq. Meter)
30
20
10
0
Hook
Wild Beach
Wash Flats


Mean Cover by Shell (%/sq. Meter)
25
20
15
10
Hook
Wild Beach

24.4%, SE = 7.47, n = 8) than nests on the Hook (mean = 13.2%, SE = 3.45, n = 25)(Figure 3.4). There were no significant correlations between hatching success and shell coverage in any nesting area in 1990 or 1991. Shell coverage and vegetation cover were minimal at Wash Flats nests in 1990 and were not measured there subsequently in 1991.

Two habitat types (Inner Beach and Outer Beach) were defined on the Hook and Wild Beach and piping plover nests were assessed for their diversity between these categories using the non-parametric Shannon Index (Table 3.13). Results of diversity testing were variable when examined for each nesting area. On the Hook, there was a low diversity of nest locations between the two categories in 1989 (J = 0.4691), i.e. most nests were found at inner beach sites, but in 1990 diversity was high (J = 0.8937) indicating that nests were more evenly divided between the two habitat categories and in 1991 diversity was moderate (0.7425). On the Wild Beach, the opposite trend was detected. Nest site diversity was very high in 1989 (J = 0.9710) and very low in 1990 (J = 0.3713). In 1991, all Wild Beach nests were found at inner beach sites (n = 8). When all nests are pooled and diversity is assessed for each year, mid-range J values are observed (0.6052 - 0.7825) suggesting that nests are more likely to be aggregated towards inner beach habitats. Piping plovers may be selecting inner beach nest sites to escape tidal flooding or due to the

proximity of inner beach sites to rich foraging areas and safe brood rearing areas.

There were significant differences in the diversity of nest site locations between the Hook and the Wild Beach in 1989 and in 1990 (Table 3.14). Similar tests in 1991 were impossible because all nests on the Wild Beach were at inner beach sites (no diversity). Piping plovers nesting on the Hook and the Wild Beach appear to employ different strategies each year when selecting nest sites according to inner beach or outer beach locations.

Based on exact proportions of habitat use to availability (Table 3.15), piping plovers utilized inner beach habitats significantly more often than expected each year when all nests were considered together ($P < 0.001$). A distinct statistical preference was detected for inner beach habitats on the Hook in all years and for all nests considered together in each year (Table 3.16). On the Wild Beach, inner beach habitats were preferred in 1990, but expected proportions were too small to allow utilization/availability testing in 1989 and 1991. Outer beach habitats were distinctly avoided in all categories tested.

Piping plovers may have realized a reproductive advantage at inner beach nest sites during the extremely wet nesting season of 1990. On the Hook, I found significantly greater hatching rates at inner beach nests in 1990 ($P = 0.0450$) and

Table 3.13. Indices of diversity between inner beach and outer beach piping plover nest locations in two beach nesting areas at Chincoteague NWR, 1989-1991.

Area	Year	No. Of Inner[1] Nests	%	No. Of Outer[2] Nests	%	H	J[3]
Hook	1989	18	90.0	2	10.0	0.1412	0.4691
	1990	20	69.0	9	31.0	0.2690	0.8937
	1991	15	78.9	4	21.1	0.2235	0.7425
Wild Beach	1989	3	60.0	2	40.0	0.2923	0.9710
	1990	13	92.9	1	7.1	0.1118	0.3713
	1991	8	100.0	0	0.0	0.0	0.0
All	1989	21	84.0	4	16.0	0.1910	0.6344
	1990	33	76.7	10	23.3	0.2355	0.7825
	1991	23	85.2	4	14.8	0.1822	0.6052

[1] Inner beach nests are closer to a marsh, mud flat, or continuous vegetation than to the ocean wrack.
[2] Outer nests are closer to the ocean wrack than to a marsh, mud flat, or continuous vegetation.
[3] J=1.0 indicates high diversity, that is, nests are distributed evenly among locations.

Table 3.14. t-tests of differences in indices of diversity between inner and outer beach nest locations at Chincoteague NWR, 1989-1991.

Sample	Year	H_1	H_2	t	P
Hook vs Wild Beach	1989	0.1412	0.2923	5.0535	< 0.001
	1990	0.2690	0.1118	4.8369	< 0.001
	1991	0.2235	0.0	----	

Degrees of freedom calculated using: $\frac{(\text{Var } H_1 + \text{Var } H_2)^2}{(\text{Var } H_1)^2/N_1 + (\text{Var } H_2)^2/N_2}$

where N_1 and N_2 are the total number of nests in samples 1 and 2 respectively (Magurran 1988).

Table 3.15. Results of G tests comparing observed vs expected ratios of piping plover nests between two nesting habitat categories at Chincoteague NWR, 1989-1991.

Area		Habitat Category: Inner Beach	Habitat Category: Outer Beach	N	G	P
1989						
Hook	Obs.	17	2	19	13.5	< 0.001
	Exp.	9.5	9.5			
Wild Beach	Obs.	3	2	5 [1]		
	Exp.	2.5	2.5			
Refuge	Obs.	20	4	24	11.6	< 0.001
	Exp.	12	12			
1990						
Hook	Obs.	20	9	29	4.3	< 0.05
	Exp.	14.5	14.5			
Wild Beach	Obs.	13	1	14	12.2	< 0.001
	Exp.	7	7			
Refuge	Obs.	33	10	43	13.0	< 0.001
	Exp.	21.5	21.5			
1991						
Hook	Obs.	15	4	19	6.8	< 0.01
	Exp.	9.5	9.5			
Wild Beach	Obs.	8	0	8 [1]		
	Exp.	4	4			
Refuge	Obs.	23	4	27	14.8	< 0.001
	Exp.	13.5	13.5			

[1] Expected frequencies must be ≥ 6 to test hypothesis.

Table 3.16. Results of Utilization/Availability tests for two opposing habitat categories at Chincoteague NWR, 1989-1991.

Area	Year	Habitat Category	
		Inner Beach	Outer Beach
Hook	1989	Preferred [1]	Avoided [2]
	1990	Preferred	Avoided
	1991	Preferred	Avoided
Wild Beach	1989 [3]		
	1990	Preferred	Avoided
	1991 [3]		
Refuge	1989	Preferred	Avoided
	1990	Preferred	Avoided
	1991	Preferred	Avoided

[1] Preferred habitats are those in which piping plover nests are found more often than expected.
[2] Avoided habitats are those in which piping plover nests are found less often than expected.
[3] Expected frequencies too small to proceed with Utilization/Availability testing.

Table 3.17. Differences in productivity and causes of egg loss at inner beach vs outer beach piping plover nest sites on the Hook and the Wild Beach at Chincoteague NWR, 1989 - 1991.

Year	Habitat Category	Nests	Eggs N	Eggs Mean	Eggs SD	Hatched N	Hatched Mean	Hatched SD	Fledged N	Fledged Mean	Fledged SD	Weather N	Weather Mean	Weather SD	Predator N	Predator Mean	Predator SD
Hook																	
1989	Inner	17	66	3.92	0.33	44	2.58	1.37	19	0.82	1.19	5	0.29	0.99	12	0.71	1.40
	Outer	2	7	3.50	0.71	7	3.50	0.71	3	1.50	0.71	0	0.0	0.0	0	0.0	0.0
	Probability [1]			P=0.1722			P=0.3196			P=0.4678							
1990	Inner	21	64	3.05	1.07	25	1.19	1.50	13	0.62	0.97	14	0.76	1.45	20	0.95	1.53
	Outer	9	19	2.11	1.27	3	0.33	1.00	1	0.11	0.33	12	1.33	1.66	4	0.44	0.73
	Probability			P=0.0660			P=0.0450*			P=0.0224*			P=0.2292			P=0.6639	
1991	Inner	20	67	3.35	0.88	43	2.15	1.79	14	0.60	2.27	0	0.0	0.0	9	0.45	0.89
	Outer	5	16	3.20	1.30	15	3.0	1.73	5	1.0	1.73	1	0.20	0.44	0	0.0	0.0
	Probability			P=1.0			P=0.3151			P=0.9078							
Wild Beach																	
1989	Inner	3	12	4.0	0.0	12	4.0	1.0	1	0.33	0.58	0	0.0	0.0	0	0.0	0.0
	Outer	2	6	3.0	1.41	4	2.0	2.83	0	0.0	0.0	0	0.0	0.0	2	1.0	1.41
	Probability			P=0.2207			P=0.2207										
1990	Inner	13	47	3.62	0.77	33	2.54	1.85	2	0.15	0.38	10	0.77	1.54	4	0.0	0.0
	Outer	1	3	3.0	0.0	3	3.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
	Probability			P=0.7518			P=0.4497										
1991	Inner	8	32	4.0	0.0	25	3.13	1.64	3	0.38	0.52	0	0.0	0.0	0	0.0	0.0
	Outer	0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
	Probability																

[1] Wilcoxon two-sample Rank Sum test, 1 df.

significantly greater fledging rates from inner beach nests in the same year (P = 0.0224)(Table 3.17). No differences were found in egg production or in egg losses to weather and predators between inner beach and outer beach nests on the Hook in any year. On the Wild Beach I observed no significant differences in productivity estimates or causes of egg loss between inner beach and outer beach nests, although in many cases, small sample sizes made significance testing impossible.

NESTING DISPERSION AND DENSITY

Nearest neighbor distances were calculated for all simultaneously active piping plover nests in each year. I determined mean nearest neighbor distances for all three nesting areas and for two sub-categories on the Hook (1) North Hook (2) South Hook. These sub-categories were based on observed differences in habitat structure (wider beaches on North Hook) and suspected differences in nesting density and dispersion.

A total of 194 piping plover nests from five nesting areas were included in the nearest neighbor analysis (Table 3.18). Nearest neighbor distances ranged from 35.1 m on the Hook in 1989 to 907.4 m on the Wash Flats in 1990. Mean nearest neighbor distances were greatest on the Wash Flats and smallest on the North Hook in all three years.

Table 3.18. Clark and Evans Nearest Neighbor analysis of piping plover nest dispersion within available nesting habitats at Chincoteague NWR, 1989 - 1991.

Area	Year	Total Nesting Area (ha)	Percent of Nesting Area	No. of Nests	Nearest Neighbor (m) Mean	SD	Range	R	Dispersion	Sig.
Hook	1989	67.74	100.0	19	131.8	96.2	35.1-348.4	1.41	Random	NS
	1990	67.74	100.0	29	144.7	81.2	37.2-277.8	1.35	Random	NS
	1991	67.74	100.0	25	157.4	81.4	55.5-314.8	1.73	Random	NS
N. Hook	1989	39.88	59.9	16	126.5	85.8	35.1-348.4	16.03	Regular	0.001
	1990	39.88	59.9	23	137.4	74.5	81.2-277.8	20.86	Regular	0.001
	1991	39.88	59.9	13	163.8	92.9	55.5-314.8	18.71	Regular	0.001
S. Hook	1989	26.67	40.1	3	159.8	163.3	65.5-348.4	1.07	Random	NS
	1990	26.67	40.1	6	173.0	106.6	37.2-259.4	1.64	Random	NS
	1991	26.67	40.1	12	447.9	612.1	111.0-277.8	5.49	Regular	0.001
Wild Beach	1989	18.89	100.0	5	239.6	122.4	100.6-426.7	2.47	Random	NS
	1990	18.89	100.0	14	328.0	245.7	111.3-925.9	5.65	Regular	0.001
	1991	18.89	100.0	8	398.1	171.6	203.6-666.7	5.18	Regular	0.001
Wash Flats	1989	159.24	100.0	6	404.2	222.6	193.6-804.7	1.57	Random	NS
	1990	159.24	100.0	10	362.4	277.9	55.5-907.4	1.82	Random	NS
	1991	159.24	100.0	12	205.1	140.0	37.0-481.5	1.13	Random	NS

I tested dispersion of piping plover nests in all years for significant departure from random dispersion expecting that any departure from random would be towards regular dispersion as a result of territorial interactions. I estimated suitable nesting habitat to be 67.7 ha on the Hook (entire), 39.9 ha on the North Hook representing 59.9% of the Hook, 26.7 ha on the South Hook representing 40.1% of the Hook, 18.9 ha on the Wild Beach, and 159.2 ha on the Wash Flats. Area estimates of suitable nesting habitat on the Wash Flats were problematic due to fluctuating water levels which influenced habitat availability.

The dispersion pattern was determined to be consistently regular only on the North Hook. The departure from random there was highly significant in all three years ($P < 0.001$) with R values ranging from 16.03 to 20.86, indicating that aggressive interactions between conspecifics were indeed influencing nesting patterns on the North Hook. Nest dispersion showed a random pattern on the entire Hook and on the Wash Flats in all three years with no significant departures detected. On the South Hook and on the Wild Beach dispersion was variable. However, dispersion on the South Hook was mostly random with a significant departure towards regular dispersion only in 1991 ($R = 5.49$, $p < 0.001$). On the Wild Beach, dispersion was mostly regular, showing significant departures from random in 1990 and 1991 ($P < 0.001$ in both years). Changes from random dispersion to regular dispersion

on the South Hook and the Wild Beach in the later years of this study are viewed as an indication that primary nesting habitat on the North Hook is becoming saturated and territorial repelling there may force more plovers into secondary habitats on the South Hook and the Wild Beach.

Single year nesting density was greatest on the North Hook in 1990 (6.82 nest/km) and lowest on the Wild Beach in 1989 (0.77 nests/km)(Table 3.19). Mean nesting density (n = 3 years) was also greatest on the North Hook and lowest on the Wild Beach. However, there were no significant differences in the mean nesting density between all nesting areas examined (ANOVA, F = 2.99, P = 0.073, df = 14). There were no significant location effects in the rates of nest predation (ANOVA, F = 2.16, P = 0.147, df = 14) or in hatching success (ANOVA, F = 1.13, P = 0.397, df = 14). There was, however, a highly significant difference in fledging success across locations (ANOVA, F = 7.92, P = 0.004, df = 14) with the highest fledging success (mean = 48.4 ± 2.0 percent chicks fledged) observed at the highest nesting density (mean = 5.1 ± 1.5 nests/km) on the North Hook. Further, the lowest fledging success (mean = 4.4 ± 0.6 percent chicks fledged) was observed at the lowest nesting density (mean = 1.4 ± 0.7 nests/km) on the Wild Beach. There was a significant positive correlation between nesting success and nesting density (Pearsons Correlation, r = 0.789, P = 0.0005, df = 1).

Table 3.19. Influence of piping plover nesting density on nest predation, hatching success, and chick survival at Chincoteague NWR, 1989 - 1991.

Area	Year	No. Nests	Density (Nests/km)	% Nests Predated	% Eggs Hatched	% Chicks Fledged
Hook	1989	19	3.38	21.1	69.3	42.3
	1990	29	5.15	34.5	39.6	44.4
	1991	25	4.44	20.0	69.9	32.8
	Mean ± SD		4.3 ± 0.9 A	25.2 ± 8.1 A	59.6 ± 17.3 A	39.8 ± 6.2 BC
North Hook	1989	16	4.74	25.0	71.4	48.9
	1990	23	6.82	33.3	39.5	50.0
	1991	13	3.86	23.1	61.9	46.2
	Mean ± SD		5.1 ± 1.5 A	27.1 ± 5.4 A	57.6 ± 16.4 A	48.4 ± 2.0 BC
South Hook	1989	3	1.32	0.0	58.3	0.0
	1990	6	2.65	33.3	20.0	16.7
	1991	12	5.31	16.7	78.0	21.9
	Mean ± SD		3.1 ± 2.0 A	16.7 ± 16.7 A	52.1 ± 29.5 A	12.9 ± 11.4 AB
Wild Beach	1989	5	0.77	20.0	92.0	4.3
	1990	14	2.17	7.1	74.1	5.0
	1991	8	1.24	12.5	78.8	3.8
	Mean ± SD		1.4 ± 0.7 A	13.2 ± 6.5 A	81.6 ± 9.3 A	4.4 ± 0.6 A
Wash Flats	1989	6	2.25	0.0	66.7	33.3
	1990	10	3.76	0.0	61.8	28.6
	1991	12	5.31	18.2	25.6	72.7
	Mean ± SD		3.8 ± 1.5 A	6.1 ± 10.5 A	51.4 ± 22.4 A	44.9 ± 24.2 BC
	F [1]		2.99	2.16	1.13	7.92
	P		0.073	0.147	0.397	0.004**
	df		14	14	14	14

[1] One-Way Analysis of Variance. Means with same letters are not significantly different (P > 0.05, Tukey HSD Multiple Comparison).

FLUSHING DISTANCE

I recorded a total of 613 flushing distances (mean = 31.6 m, SD = 25.4 m, range = 2 - 300 m) for piping plovers from 112 nests (Figure 3.5). Of these, 399 (65.1%) were 30 m or less. Only one bird was observed to flush from the nest at a distance greater than 120 m.

There were no significant differences in flushing distances between nesting areas within years ($P > 0.05$ in all years)(Table 3.20). Mean estimated flushing distances were greater, however, in 1989 than in 1990 or 1991 in all nesting areas and the differences were significant in all nesting areas (Table 3.21). These differences may be explained by the variation in observers from year to year and their abilities to estimate distance.

I estimated the minimum area required for undisturbed nesting by calculating the area of a circle with the nest at the center and the mean recorded flushing distance as the radius for each nesting area in each year (Table 3.22). Minimum area requirements ranged from 0.19 ha/pair to 0.72 ha/pair. I found an average minimum area requirement of 0.33 ha/pair for all years.

Figure 3.5. Frequency distribution of flushing distances for incubating piping plovers at Chincoteague NWR, 1989 - 1991. n = 613 observations from 112 nests.

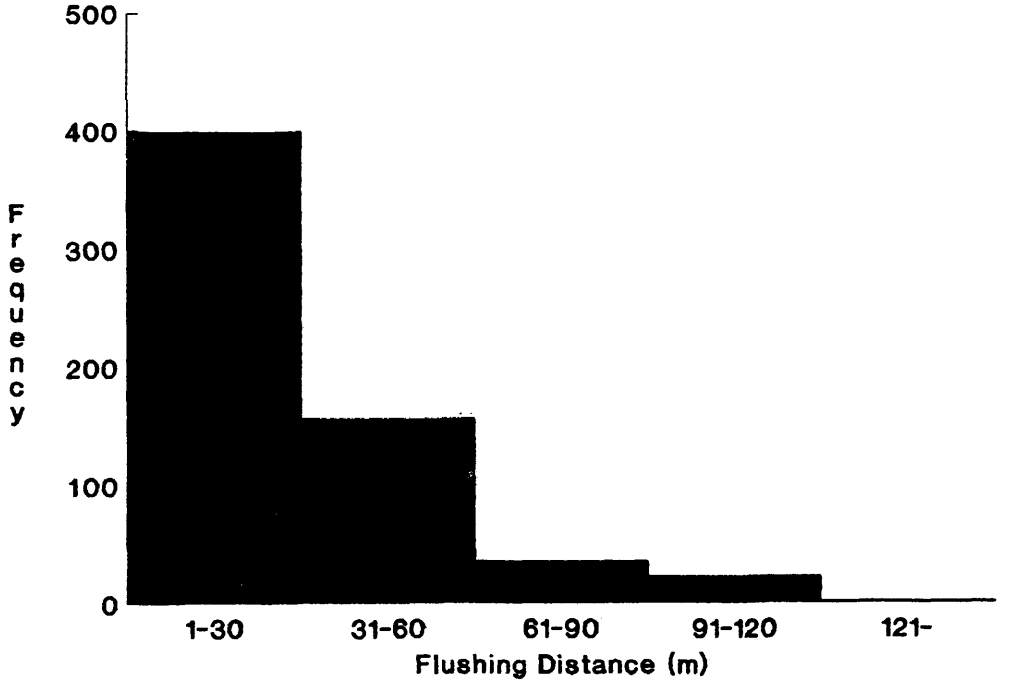

500
400
300
200
100
0
Frequency
1-30
31-60
61-90
91-120
121-
Flushing Distance (m)

Table 3.20. Comparisons [1] of flushing distances of incubating piping plovers between nesting areas at Chincoteague National Wildlife Refuge, 1989 - 1991. Number of nests = 27, 1989; 44, 1990; 41, 1991.

	Flushing Distance (m)								
	1989			1990			1991		
Area	N	Mean	SE	N	Mean	SE	N	Mean	SE
Hook	125	48.0 A	3.20	106	24.40 A	1.73	128	24.37 A	1.50
Wild Beach	24	46.79 A	3.57	78	23.92 A	1.91	54	24.67 A	1.66
Wash Flats	31	47.06 A	5.57	30	24.13 A	3.68	37	31.76 A	4.0
		F = 0.056 P = 0.945 df = 181			F = 0.035 P = 0.996 df = 215			F = 2.531 P = 0.082 df = 218	

[1] One-Way Analysis of Variance
Means with same letters are not significantly different (P > 0.05, Tukey HSD Multiple Comparison).

Table 3.21. Comparisons [1] of flushing distances of incubating piping plovers between nesting years at Chincoteague National Wildlife Refuge, 1989 - 1991. Number of nests = 27, 1989; 44, 1990; 41, 1991.

	Flushing Distance (m)								
	Hook			Wild Beach			Wash Flats		
Year	N	Mean	SE	N	Mean	SE	N	Mean	SE
1989	125	48.0 A	3.20	24	46.79 A	3.57	31	47.06 A	5.57
1990	106	24.40 B	1.73	78	23.92 B	1.91	30	24.13 B	3.68
1991	128	24.37 B	1.50	54	24.67 B	1.66	37	31.76 AB	4.0
	F = 34.795 P < 0.001 df = 358			F = 20.901 P < 0.001 df = 155			F = 6.273 P = 0.003** df = 97		

[1] One-Way Analysis of Variance
Means with same letters are not significantly different (P > 0.05, Tukey HSD Multiple Comparison).

Table 3.22. Estimated minimum area required for undisturbed nesting for piping plover derived from mean flushing distances at Chincoteague NWR, 1989 - 1991.

Area	Year	No. of Nests	Minimum Area[1] Required For Undisturbed Nesting (ha)
Hook	1989	18	0.72
	1990	21	0.19
	1991	24	0.19
Wild Beach	1989	5	0.69
	1990	13	0.18
	1991	8	0.19
Wash Flats	1989	4	0.70
	1990	10	0.20
	1991	9	0.32
Refuge	1989	27	0.70
	1990	44	0.19
	1991	41	0.21
	1989-1991	112	0.33

[1] Area calculated using πr^2 with mean flushing distance as the radius of the circle.

DISCUSSION

Although there are a wide diversity of beach nesting habitat types present, I did not measure the relative abundance of habitat types at Chincoteague NWR. Nesting habitat on the Hook, for example, is composed largely of flat berms. Only sparse blowout habitat is present there due to an intermittent primary dune system. On the Wild Beach, the primary dune system is continuous but man-made and, therefore, stable and rarely breached. This results in few blowouts and very little backdune nesting habitat. Beaches there are narrow. Piping plovers nesting on the Wild Beach used significantly narrower beaches than on the Hook ($P < 0.001$). Thus, plovers may be encouraged to nest on foredune slopes on the Wild Beach as a compromise between avoidance of seaward flooding and unavailability of backdune areas.[1]

Narrow beaches may represent sub-optimal piping plover breeding habitat for several reasons. Predators may be more successful at locating piping plover nests on narrow beaches than on wider ones. Nests on narrow beaches may also be more susceptible to storm and flood damage (Haig and Oring 1985, Gaines and Ryan 1988, Nordstrom 1990). The width of the beach

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[1] Backdune habitats on the Wild Beach may often be unsuitable as nesting habitat, rather than unavailable, if backdune foraging sites for adults and pre-fledged young are absent. Stabilized dunes may prevent the formation of moist soil flats often used as foraging sites close to nesting sites.

may fix the distance at which approaching predators are detected and influence the effectiveness of nest defense behaviors. Brunton (1986) suggests that in order to minimize risk to incubating killdeer and discovery of their nests, the incubating bird must become aware of the predator at a "safe distance".

In all three years of this study, I found more berm nests (31.8%, n = 219) than any other category of nesting habitat, however, I find it interesting that the percentage of berm nests on the Hook decreased each year. Burger (1987) observed that piping plovers at Corson's Inlet, New Jersey shifted nest locations closer to dunes in response to escalating predator pressure. Piping plovers on the Hook shifted to backdune nest sites during this study, probably as a result of increasing mammalian and avian predator pressure. Alternatively, backdune nesters may have been attempting to avoid flooding or may have been responding to increased disturbance associated with the management procedure of placing predator exclosures on all nests.

Piping plover breeding habitat consists primarily of open sandy beaches, although a variety of habitats provide suitable sites (Haig 1992). In the Great Plains, piping plovers use sand, gravel, and alkaline shores of rivers and lakes as breeding sites (Cairns 1977, Whyte 1985, Gaines and Ryan 1988). At Brigantine Beach in New Jersey, Burger (1987) found plovers nesting closer to dunes and vegetation, and on flatter

spots with more shell cover than was present at random points. Further nest site requirements include refuge from disturbance and predators and access to intertidal foraging sites for adults and young.

At his study site in Massachusetts, Strauss (1990) found 75% (n = 80) of all nesting attempts from 1984 to 1987 located seaward of the primary dunes either in blowouts or on sandspits. The remaining 25% of all nesting attempts were found behind the primary dune line, between mature sand dunes. Also in Massachusetts, MacIvor (1990) observed 41% of all nests (n = 219) were located in berm habitats with the next largest percentage (19%) of nests found in interdune habitats. Only 14% and 6% of all nests were found in overwash and blowout habitats respectively. She attributes the low use of overwash habitats in her study to habitat changes associated with vegetation encroachment.

I observed greater than expected hatching success in ephemeral, sparsely vegetated berm habitat on the Hook in all three years and no significantly greater hatching success at backdune nests there. On the Hook, piping plovers in this study may have been unsuccessful in improving their reproductive success by shifting away from berm nesting habitat. MacIvor (1990) believes that piping plovers increased their chance of nest survival and therefore improved reproductive success by nesting in dense vegetation. MacIvor (1987) observed increased levels of predation and overwash

associated with nest sites in ephemeral, un-vegetated beach sections.

On the Wild Beach, piping plovers selected berm habitats more often than any other habitat, but also selected more backdune and blowout habitats each year. In this case, however, the shift to backdune habitats was rewarded with greater than expected hatching success in 1990. On the Wild Beach, backdune habitats, although scarce, provided some survival advantage to nesting piping plovers during incubation although the advantage was lost during brood-rearing, probably due to inadequate foraging resources.

These data suggest that wide, open, berm habitats are important and productive sites for nesting piping plovers at Chincoteague NWR, but that backdune habitats may afford a viable alternative to berm sites when physical or biological disturbances to typical nest site selection are operating. Areas that lack habitat mosaics suitable to allow species to adjust their distribution and behavior in response to disturbance may experience high extinction probabilities (Karr 1982). The combined effect of the lack of open berm habitat on the Wild Beach and the functional unavailability of backdune habitat there may result in consistently low reproductive success for that area typical of "sink" habitats where within-habitat reproductive success is insufficient to balance local mortality (Pulliam 1988). These results further suggest that artificial dune stabilization on the Wild Beach has limited

piping plover nesting habitat and reproductive success. Although this practice is no longer maintained on the Wild Beach, piping plover populations there will likely not be viable until natural forces re-create suitable nesting conditions.

Higher elevations may impart some protection to piping plover nests against flooding (MacIvor 1990), but I could not prove that piping plovers selected higher sites first. The selection of nests according to their height presumably occurs with no apriori knowledge by the bird of where flooding will occur and may be more related to predator vigilance than to flood protection.

Piping plovers add shell lining to their nest scrapes during courtship, but nests constructed in sandy substrates may or may not have shell linings (Haig 1992). Aside from their function in ritualized courtship behavior, shell bits may aide nest drainage or enhance nest crypsis (Cairns 1977, Sidle 1984a). Patterson et al (1991a) did not detect any significant differences in the mean percent composition of sand and shell bits at nest substrates between predated piping plover nests and other piping plover nests in the Virginia portion of their study site on Assateague Island in 1986 and 1987. Further, they observed no significant difference in the mean percent vegetation cover between predated piping plover nests and other piping plover nests on Assateague Island in Maryland and Virginia. MacIvor (1990) observed significantly

greater percent shell cover and percent beach grass cover at piping plover nests than at non-nest sites in Massachusetts.

In this study, the use of shell cover at piping plover nest sites was highly variable between nesting areas and between years; however, it did not influence hatching success. Vegetation cover, on the other hand, increased at nest sites on the Hook and the Wild Beach between years. This is also interpreted as a response to predator pressure which increased throughout the study. Vegetation cover was positively correlated with hatching success on the Hook only in 1990. Page et al (1985) suggested that where objects on the beach are abundant, they may help conceal movements of snowy plovers to and from the nest. Vegetation cover probably helps to hide the movement of adults to and from the nest during incubation exchanges and, therefore, prevents divulging the nest location to potential predators.

I suggest that predator exclosures may signal the location of nests to predators in areas of dense vegetation where the nest may have remained hidden from predators without the exclosure. This may be especially true of avian predators traversing to and from open beach areas. Mammalian predators, relying on scent cues, may locate nests easily despite the use of cover. I recommend cautious use or discontinuing the use of predator exclosures where vegetation cover exceeds 50% coverage per square meter at the nest if avian predation has been identified as a problem.

Dispersion of piping plover nests throughout available nesting habitat appears to be mostly influenced by the territorial interactions of neighboring pairs as indicated by regular spacing in the most densely populated area on the North Hook. Departures from random spacing also occurred on the Wild Beach and the South Hook indicating that the placement of nests there was influenced by the placement of other nests. Grover and Knopf (1982) observed that the distribution of snowy plover nests at Salt Plains National Wildlife Refuge in Oklahoma was clumped near streams or standing bodies of water. Mean nearest neighbor distance for snowy plovers was 100.8 ± 108.9 m. They attributed the clumped dispersion to the abundance of prey (shore flies, genus Ephydra) along the stream edges. Burger (1987) working at Brigantine Beach, New Jersey, observed piping plover nests from 85 to 99 m from other piping plover nests. Bergstrom and Terwilliger (1987) observed regular spacing among piping plovers nesting on Metompkin Island in Virginia and suggested that intraspecific aggression and, to a lesser extent, interspecific aggression with the congeneric Wilson's plover were operating to space out nest locations. Mean nearest neighbor distance for piping plovers on Metompkin Island was 138 ± 89 m. Regular spacing may result from individual interactions and may function to partition resources and avoid predators. Predation seems to promote spacing out in prey

species whose main defense is to avoid detection (Anderson and Wiklund 1978).

Dispersion of animals spatially may also be a response to habitat features as well as the presence or absence of conspecifics (Hinde 1956, Brown and Orians 1970). Further, as habitat specialists, piping plovers may occupy only a small portion of habitat patches in a given area with further reductions if patch interiors are selected rather than edges (Weins 1985). Piping plovers showed a distinct preference for inner beach habitats in this study, selecting them significantly more often than equally available outer beach habitats. Estimates of dispersion may have been influenced by the preference for inner beach habitats. Inner beaches likely represent the interior of habitat patches for piping plovers, providing nesting territories strategically positioned close to profitable foraging areas and well protected brood-rearing areas.

Predation of piping plover nests is greater when plover nests are located within nesting colonies of least terns (Sterna albifrons)(MacIvor 1990) and may be due to greater advertisement of their location to potential predators (Strauss 1990). Page et al (1983) found predation on snowy plovers (Charadrius alexandrinus) nesting at Mono Lake to represent 40% of all nest attempts and suggested that reproductive success was inversely proportional to internest distance. Snowy plovers nesting at Mono Lake demonstrated

higher hatching and fledging success when nesting at lower densities.

I observed higher nest predation in piping plovers where nesting density was highest. Hatching success was greatest at low density sites on the Wild Beach. But, fledging success was much greater on the Hook and North Hook where density was high than on the South Hook and Wild Beach where density was low.

Two main anti-predation strategies for ground-nesting birds have been proposed by Picman (1988). The first strategy focuses on defense by avoiding predator attacks and involves strategies such as concealment of the nest and spacing out to reduce conspicuousness of nesting. The second strategy favors a colonial pattern of nesting to exploit the advantages of communal anti-predator attacks and dilution of predator effects.

Piping plovers exhibit much variation in nesting density. Elias-Gerken (1994) observed densities ranging from 0.2 pairs per km on Fire Island to 2.1 pairs per km on Westhampton Island within her study area on New York's central barrier islands. High density or semi-colonial nesting of piping plovers requires a departure from the typical Charadrii nest defense strategy of spacing out nests. As a result nest loss can be catastrophic when flooding occurs or when predators find many nests in one location. However, chicks may be better protected allowing higher productivity at high density sites by mobbing of avian predators (see chapter 2) and through an

early warning system against predators or intruders which prevails when nesting pairs are concentrated. Communal defenses against approaching predators in semi-colonial nesting systems may allow pre-fledged chicks enough time to seek cover while providing no similar benefits to stationary egg clutches.

Wildlife managers may find the greatest potential for improvements to piping plover reproductive success in high density, semi-colonial nesting situations. Greater fledging success observed in such areas might be utilized to the fullest extent if predator exclosures or other egg protection measures are used to enhance depressed hatching success.

Piping plovers show a high degree of site fidelity and may benefit from this behavior through increased familiarity with local resources. However, a lack of other available breeding sites may also influence return patterns (Haig 1988a). In the northern Great Plains, Gaines and Ryan (1988) found evidence that habitat for piping plovers may be a limiting factor. They noted a substantial increase in breeding pairs associated with an increase in availability of habitat and suggested that plover populations there could be stabilized or increased by creating high quality nesting habitat.

Patterson (1980) proposes that territorial behavior, especially territory size, varies in relation to the environment and that the effect is to adjust density to

variations in the environment. Habitat quality, however, must be defined as a product of density and reproductive success (Van Horne 1983, Vickery et al 1992). I believe that availability of habitat may be even more limiting due to the territorial repelling of breeding pairs. Observed regular spacial patterns even at high nesting density suggests that some birds may be forced out of high quality habitats where reproductive success is higher and into lower quality sites where density is lower and reproductive potential is also lower. This suggests that improvements to secondary habitats where nesting success and density are low (e.g. Wild Beach) may be another effective means of aiding population recovery.

Defended territory size varies substantially in plovers; 1.6 ha in white-fronted plover (Charadrius marginatus)(Summers and Hockey 1980), 0.5 ha in little ringed plover (Charadrius dubius)(Simmons 1956), 16.0 ha in mountain plover (Charadrius montanus)(Graul 1973a). Minimum areas required for undisturbed nesting, calculated in this study, are similar to defended territories but territories are defended against conspecifics. Flushing from the nest as a response to human intruders is more likely an attempt to conceal the nest as a form of predator avoidance (Byrkjedal 1987).

Reported mean flushing distances for piping plovers are as little as 24 m (n = 31) in Massachusetts (Hoopes 1993). Cross and Terwilliger (1993) observed a mean flushing distance of 63 m (n = 201) at multiple barrier island sites in Virginia

from 1986 - 1991. Loegering (1992) observed a mean flushing distance of 78 m (n = 43) at his study site on Assateague Island, Maryland and recommended a 225 m disturbance buffer based on the greatest mean flush distance (174 m) and his estimated minimal agitation distance (50 m).

I believe that our three year mean estimated minimum area required for undisturbed nesting (0.33 ha) probably underestimates the area requirement necessary to protect all piping plovers at Chincoteague NWR. Many plovers in this study were likely habituated to our approach throughout the term of their incubation resulting in decreased flushing distances. Further, the use of vehicles by researchers to approach nests when constructing predator exclosures may have obscured incubating plovers' views of human shapes and biased flushing distances. I recommend using the maximum flushing distance, instead of the mean, to ensure full protection to all breeding plovers at this site. I recorded only one flushing distance above 120 m and, therefore, suggest the use of 120 m as a radius to calculate a minimum circular undisturbed nesting area requirement of 4.55 ha.

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